UNIVERSITÉ DU QUÉBEC À MONTRÉAL

REPRODUCTION COOPÉRATIVE CHEZ L'ARAÇARI VERT *(PTEROGLOSSUS VIRIDIS)* AU BIODÔME DE MONTRÉAL

MÉMOIRE

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JEAN-PHILIPPE GAGNON

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AVANT - PROPOS

Ce mémoire a été rédigé sous la forme de deux articles scientifiques écrits en anglais. Il comporte une introduction et une conclusion générale en français. En tant que candidat à la maîtrise, j'ai effectué la récolte des données et visionné la totalité des vidéos sur lesquels portent ces articles. J'ai également analysé les données en suivant les conseils de mes co-directeurs et j'ai rédigé les deux articles à titre de premier auteur. Pierre Drapeau et Frédérique Dubois, co-directeur(trice), en sont les deuxième et troisième auteurs respectivement. Pour souligner sa contribution à l'étude, Serge Parent y figure comme quatrième auteur. Il a facilité la mise en place du projet au Biodôme en plus de faire de nombreuses suggestions au sujet de mes travaux de recherche. Les manuscripts : "Quantitative assessment of cooperative breeding behaviour of the Green Aracari (*Pteroglossus viridis),* a cavity nester in captivity " et "High cavity availability does not prevent cooperative breeding of a Green Aracari (*Pteroglossus viridis*) family in captivity" seront soumis à des revues scientifiques arbitrées.

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RÉSUMÉ

La coopération à la reproduction est rarement observé chez les oiseaux. Toutefois, lors de la reproduction, il arrive qu'on assiste à des comportements coopératifs propres à l'espèce et dont l'expression peut être favorisée par des contraintes écologiques. Les études sur la reproduction coopérative des oiseaux ont principalement portées sur des espèces à nid ouvert, si bien que très peu d'informations sont disponibles sur la reproduction coopérative des espèces cavicoles. La conservation des espèces en captivité nécessite une connaissance approfondie des comportements de reproduction afin d'offrir les meilleurs conditions pour qu'une espèce connaisse un bon succès de reproduction. L'Araçari vert *(Pteroglossus viridis)* est un petit toucan d'Amérique du sud qui est reproduit en captivité par plusieurs institutions zoologiques nord américaine. En nature, des signes d'une reproduction coopérative ont été observé chez trois espèces d'aracaris, mais ce comportement n'a pas encore été étudié en captivité. Cette étude a pour objectif de décrire les comportements coopératifs observés lors de la reproduction d'une famille d'Araçari vert sur deux événement de reproduction (2008, 2009). Dans le premier chapitre de ce mémoire, nous décrivons en détail la participation des individus aux comportements associés à la reproduction : l'aménagement du nichoir, l'incubation des œufs, l'entretien du nichoir, l'efficacité dans l'approvisionnement des oisillons ainsi que la durée des visites. La femelle contribue majoritairement aux soins des oisillons, le mâle participe peu mais sa présence pourrait être associée à des comportements de surveillance, tandis que les juvéniles (assistants) ne participent qu'à l'alimentation des oisillons. Dans le second chapitre nous concentrons les observations sur l'alimentation des oisillons. Au total, cinq individus (femelle, mâle et 3 juvéniles) ont été observés à l'aide d'une caméra infrarouge située à l'intérieur d'un nichoir. Nous avons mesuré la fréquence des visites et la fréquence d'alimentation des oisillons selon leur âge ainsi que le moment de la journée pour deux événements de reproduction. Le mâle participait peu à l'alimentation des oisillons tandis que les assistants ont suivi les mêmes tendances que la femelle, la principale approvisionneuse. La contribution du mâle et des assistants diminue en 2009, mais celle de la femelle reste constante indiquant que les variations dans l'alimentation des oisillons ne sont pas compensées par celle-ci. Cette recherche présente pour la première fois les comportements reproducteurs coopératifs de l'Araçari vert.

Mots clés : Araçari, nicheur cavicole, comportement, coopération, reproduction, captivité, parents, assistants.

ABSTRACT

Cooperative breeding is rarely encountered in birds. However, particular ecological constraints may enhance the expression of cooperative behaviours for these organisms. Studies on cooperative breeding in birds have been mainly conducted on species using open-cup nests, and accordingly there is paucity of knowledge on this behaviour for cavity nesters. Bird conservation in captivity with the objective of providing suitable breeding conditions to captive birds requires in depth knowledge of their breeding behaviour to increase the chances of successful breeding. The Green Aracari (*Pteroglossus viridis*), a small South American toucan, is a cavity nester reared in captivity by many zoological institutions throughout North America. Sings of cooperative breeding behaviour in nature has been observed on three different species of aracari but it has not been studied in captivity yet. This study describes for the first time the cooperative breeding behaviour of the Green Aracari in captivity during two breeding events (2008, 2009). In the first chapter, we quantified the participation of individuals associated with cooperative breeding behaviours throughout the entire breeding cycle including nest preparation, eggs incubation, nest maintenance, provisioning efficiency and visits' duration. The female was the main contributor to the overall care of the nestlings while the male was a poor provider but its frequent attendance at the nest suggests that it may be associated to surveillance behaviours. Juveniles (helpers) only took part to the feeding of the nestlings. In the second chapter, we focus on the relative contributions of cooperative participants to nestlings' feeding. A total of five individuals (female, male and 3 juveniles) were followed with infrared camera inside the nesting box. We measured the visiting rate of parents and helpers and nestlings' feeding rate as a function of the age of nestlings and the daily period for the two breeding events of this study. The male's contribution was constantly lower than the helpers and the females over the two breeding events. Helpers were following the same feeding assistance pattern of the female, the main provider. However, contributions of the male and the helpers were less important in 2009, but the female's provisioning behaviour remained the same indicating that variation in feeding rates by helpers were not compensated by the female.

Keywords: Aracari, cavity nester, behaviour, cooperation, breeding, captivity, parents, helpers

INTRODUCTION

La reproduction coopérative

Plusieurs espèces animales utilisent des comportements coopératifs lors de leur reproduction, mais dont la complexité varie selon le groupe. Par exemple, on retrouve des comportements élaborés chez les mammifères où l'organisation sociale est développée, comme chez les primates, les canidés, les viverridés et les rongeurs. Les oiseaux quant à eux diffèrent des mammifères dans la forme des soins primaires (l'approvisionnement chez les oiseaux par rapport à l'allaitement chez les mammifères), ce qui a un effet majeur sur l'expression des comportements en reproduction coopérative (Solomon and French 1997).

Plusieurs éléments peuvent faire varier l'expression des comportements coopératifs. La composition du groupe aura un impact sur la nature de la coopération chez le Tamarin à selle (*Saguinus fuscicollis*) où les groupes de 2 mâles en coopération réciproque ont un meilleur bilan de reproduction comparativement aux mâles monogames (Terborgh and Goldizen 1985). Chez les insectes sociaux où la définition des rôles chez les individus est structurée, on observe aussi des variations comportementales en fonction du rang. Ainsi chez la guêpe à papier (*Polistes dominulus*), plus le rang occupé par l'individu au sein du groupe est élevé, moins les comportements coopératifs seront intenses (Cant and Field 2001). On reconnait également qu'une dynamique familiale peut varier selon les opportunités qu'offre le milieu, comme c'est le cas chez le cichlidé *Neolamprologus pulcher,* un poisson africain (Terborgh and Goldizen 1985).

La reproduction coopérative est un comportement rare chez les oiseaux. Cette forme d'aide au nid est documentée chez seulement 308 des 9672 espèces d'oiseaux soit 3,2 % (Arnold and Owens 1998). Ce système de reproduction assisté est toutefois retrouvé chez 88% des espèces aviaires qui vivent en groupes familiaux (N.J.

Demong, unpublished compilation). La reproduction coopérative serait donc restreinte aux unités familiales (Emlen 1995) . Par contre, nous ne savons pas encore pourquoi les frugivores vivent rarement en unités sociales permanentes et ne se reproduisent pas de manière coopérative, même s'ils ont tendance à former des groupes (Restrepo and Mondragòn 1998). Chez les oiseaux on définit la reproduction coopérative par la présence d'individus non reproducteurs faisant partie d'un groupe social et qui participent à nourrir et à défendre des jeunes qui ne sont pas leurs propres descendants (Emlen 1982b, Ligon and Stacey 1991, Arnold and Owens 1999, Ekman 2006). Plusieurs espèces à reproduction coopérative ont fait l'objet d'études qui permettent de mieux comprendre les mécanismes qui sont en cause dans de telles situations (Brown 1987, Stacey and Koening 1990, Koenig and Dickinson 2004). Une des premières études sur le sujet fut celle de Woolfenden et Fitzpatrick qui eut cours de 1970 à 1979. Ce qui avait débuté comme un simple recensement ornithologique d'une station de biologie se transforma en une étude démographique approfondie d'une espèces coopérative : le Geai buissonnier de Floride (*Aphelocoma coerulescens*) (Woolfenden and Fitzpatrick 1984). Ils ont, entre autres, mis en évidence que le manque de ressources alimentaires et des sites favorables à la nidification agissent comme des facteurs qui limitent la dispersion des juvéniles. Cette dispersion est différée lorsque les juvéniles demeurent sur le territoire parental plutôt que de chercher à coloniser un nouveau territoire et à se reproduire eux-mêmes. Certains individus qui retardent leur dispersion ont un meilleur taux de survie (Kokko and Ekman 2002). Dans pareille situation, il arrive qu'on assiste à une participation des juvéniles aux soins des oisillons qui proviennent d'adultes apparentés.

Les individus non reproducteurs qui coopèrent peuvent retirer des gains indirects en valeur adaptative (Khan and Walters 2002, Williams and Hale 2006). Par exemple, lorsqu'un membre de la famille améliore le succès reproducteur de ses parents par des soins prodigués aux oisillons (Rabenold 1985). La coopération s'explique alors par le mécanisme de sélection de parentèle. Ce gain pourrait également se traduire par un apprentissage des soins parentaux qui permettrait un meilleur succès

reproducteur de l'assistant lorsqu'il sera lui-même en situation de reproduction (Mumme et al. 1990). Il s'agit alors de gain direct retardé.

La dispersion différée, prémisse à la coopération

La dispersion joue un rôle critique dans la structure et la dynamique d'une population d'oiseaux (Walters 2000). En nature, les juvéniles ne se dispersent pas toujours systématiquement suite au sevrage (Russell et al. 2004). Chez plusieurs espèces coopératives, les assistants sont des juvéniles qui ont différé leur dispersion (Doerr et Doerr, 2007) ou des adultes qui ont échoué leur reproduction (Russell 2001). Certains mécanismes maintiennent la présence des juvéniles sur le territoire des parents, tels que les contraintes écologiques, une prédisposition naturelle de l'espèce (Arnold and Owens 1999) ou encore des parents népotistes (Ekman et al. 2001a).

Trois contraintes écologiques peuvent retarder la dispersion des juvéniles d'une espèce aviaire : la disponibilité ou la productivité d'un territoire, la disponibilité d'un site de nidification adéquat et l'accès à un partenaire sexuel (Emlen 1982b, Kokko and Lundberg 2001, Kokko and Ekman 2002, Cockburn 2003, Ekman 2006). Par exemple, chez le Pic à face blanche (*Picoides borealis*), la disponibilité des cavités est le facteur déterminant dans la dispersion des juvéniles (Walters et al. 1992a). Cette espèce utilise des cavités pour sa reproduction et pour le gîte. L'accès à cette ressource est difficile parce que l'espèce creuse des trous dans des arbres sains et l'excavation peut prendre plusieurs mois (Lennartz et al. 1987). La disponibilité et la distribution des cavités est donc une contrainte écologique qui limite la dispersion des juvéniles et conduit cette espèce à une reproduction coopérative (Walters et al. 1992a).

Les juvéniles qui ne trouvent pas de cavités adéquates pour le gîte ou éventuellement la nidification restent sur le territoire parental au sein de leur cellule

familiale. Les études sur la coopération aviaire appuient l'idée qu'un bénéfice de valeur adaptative est généré par une dispersion différée, un concept également appelé «bénéfice philopatrique» (Stacey and Ligon 1991).

La dispersion différée des juvéniles peut également être un comportement intrinsèque de l'espèce selon ses origines évolutives ou son histoire naturelle (Walters et al. 1992b, Kokko and Lundberg 2001, Ligon and Burt 2004). La variation écologique est le facteur clé qui détermine quelles espèces, ou populations d'une lignée donnée, adopteront un comportement coopératif à la reproduction (Arnold and Owens 1999). On retrouve davantage de coopération dans les groupes familiaux que dans les groupes d'individus non apparentés (Emlen 1995). Ainsi certaines familles d'oiseaux seront plus susceptibles de montrer de la coopération sous des conditions écologiques favorables (Ligon and Burt 2004). Plusieurs ramphastidées, en particulier les aracaris, forment des groupes familiaux pour plus d'une année. Cet indice porte à croire que l'Araçari vert aurait une histoire naturelle favorable à l'expression de comportements coopératifs dans un milieu où les contraintes écologiques seraient contrôlées expérimentalement.

La présence de juvéniles sur le territoire parental peut également venir d'un comportement népotiste. Un parent qui concède l'accès à la nourriture à ses descendants mais qui la refuse aux autres (Verbeek and Butler 1981). Dans ce contexte, les individus qui demeurent sur le territoire parental ont un meilleur taux de survie et donc de meilleures chances de se reproduire la saison suivante même s'ils n'améliorent pas le succès reproducteur des parents (Ekman et al. 2001a). La survie de la descendance, qui sous-tend leur éventuel succès reproducteur, représente une valeur adaptative accrue pour le parent, d'où l'expression des comportements népotistes.

Dans l'éventualité où un individu ne retarde pas sa dispersion, mais n'arrive pas à s'établir sur un territoire, il devient un «flotteur» dans la population. Cette situation n'est pas souhaitable car les coûts associés sont supérieurs à ceux d'un individu qui

reste au sein du groupe et qui ne coopère pas à la reproduction du couple dominant (Ridley et al. 2008).

Bénéfices indirects

L'amélioration du succès reproducteur et la survie d'un parent, sont des bénéfices indirects qui peuvent contribuer à accroître la valeur adaptative d'un assistant. La règle d'Hamilton, utilisée pour expliquer les comportements altruistes, stipule qu'un assistant devrait aider seulement quand rB > C (Heinsohn 2004). Toute unité de soin engendre un coût (C) pour l'individu qui aide et produit un bénéfice (B) pour celui qui la reçoit. L'assistant peut également en retirer un bénéfice indirect qui est proportionnel à son degré de parenté (r) avec l'individu aidé. Cette théorie est assortie de prudence quant à l'interprétation du rôle que jouent les liens parentaux dans les gains en valeur adaptative (Dawkins 1979, Griffin and West 2002). Toutefois, il est généralement admis que pour avoir une situation de coopération, il faut que les bénéfices associés au comportement d'aide soient supérieurs aux coûts et qu'un lien de parenté soit présent (Fletcher et al. 2006, Foster et al. 2006). Cette situation est équivalente pour chaque individu d'un même niveau parental. Chez les espèces diploïdes, le degré d'apparentement entre le parent et le descendant est de 0,5 puisque le matériel génétique de l'individu provient à parts égales des deux parents. Puisque les juvéniles (assistants) sont soumis au même degré d'apparentement avec leurs parents, ils peuvent en retirer des bénéfices comparables lors d'une reproduction coopérative.

Chez certaines espèces, les parents qui sont assistés, ont un meilleur succès reproducteur (Brown et al. 1982, Blackmore and Heinsohn 2007). Chez d'autres, la production d'oisillons ou leur survie ne semble pas influencée (Eguchi et al. 2002, Canario et al. 2004). Si le nombre de descendants n'est pas accru, par contre les coûts individuels associés aux soins parentaux sont réduits parce que partagés entre les membres de la famille. Par exemple, chez le Mérion superbe (*Malurus*

cyaneus), les femelles pondent des œufs plus petits lorsqu'elles sont assistées. Elles utilisent les assistants pour obtenir des bénéfices ultérieurs, comme le nourrissage des oisillons, plutôt que d'améliorer leurs bénéfices courants de reproducteur (Cockburn et al. 2008). Dans le cas de la Gallinule poule d'eau (*Gallinula chloropus*) ce ne sont pas tous les juvéniles qui assistent et le niveau d'aide offert varie d'un individu à l'autre (Eden 1987). La charge des soins serait donc partagée inégalement entre les parents et les assistants.

En situation de coopération, on reconnaît que les assistants perçoivent des bénéfices indirects lorsqu'ils augmentent la productivité de la nichée parentale (Ekman 2006). Un individu qui n'assiste pas et ne se reproduit pas n'aura aucun gain de valeur adaptative associé à la reproduction. Pourtant, chez le Mésangeai imitateur (*Perisoreus infaustus*), les juvéniles sont retenus sur le territoire natal jusqu'à deux saisons de reproduction, mais ne sont pas admis à moins de 25 mètres du nid parental (Ekman et al. 1994, Dickinson and Hatchwell 2004). Cette rétention des juvéniles nous permet de croire qu'un bénéfice philopatrique existe, comme un meilleur taux de survie, même si les juvéniles ne participent pas aux soins parentaux. Au sein d'une population, la rétention des jeunes sans participation coopérative est plus propice sur les territoires de haute qualité (Kokko and Lundberg 2001).

Bénéfices directs retardés

L'aide peut être compensatoire lorsque les parents réduisent leur charge en soins, additive lorsqu'ils la maintiennent ou intermédiaire entre ces situations (Hatchwell et al. 1999). L'effort investi dans les soins apportés aux oisillons correspond aux coûts associés à ces comportements altruistes. Le délai encouru par une dispersion différée est également considéré comme un coût dans l'équation puisqu'il suppose qu'un individu se prive de se reproduire. Toutefois ce coût peut être compensé par la

longévité de l'espèce dans la mesure où un individu qui a retardé sa dispersion aura plus tard un meilleur succès reproducteur, d'où un bénéfice retardé.

Parmi les bénéfices recherchés par les assistants, notons l'amélioration du prestige social, le legs du territoire et l'apprentissage des soins (développement de l'habileté) pour leur propre reproduction (Heinsohn 2004). Le prestige social correspond à un individu qui améliore sa situation au sein d'un groupe en démontrant ses capacités parentales. L'individu aura de meilleures chances de trouver un partenaire, d'où une valeur adaptative accrue (Carlisle and Zahavi 1986, Zahavi 1995). Le legs du territoire débute par la reproduction du couple dominant qui tolère la présence d'un individu moyennant un "paiement de loyer" : assister le couple dans leur reproduction. L'assistant peut également obtenir une occasion de reproduction s'il participe à augmenter le succès reproducteur du dominant (Kesler et al. 2007). Éventuellement, un assistant peut hériter du territoire parental. Un meilleur taux de survie est à l'origine de ce comportement, mais il peut également se transformer en succès reproducteur accru après l'héritage du territoire parental (Khan and Walters 1997). L'apprentissage des soins parentaux est un aspect important. Lors d'une assistance à la reproduction, la qualité des soins a peu d'impact puisque la charge parentale est partagée. Cette situation est idéale pour qu'un individu développe ses habiletés. Pourtant, on a observé, chez le Pic à face blanche (*Picoides borealis*) que les individus ayant assisté leurs parents n'ont pas eu un meilleur succès de reproduction que ceux qui n'ont pas assisté leurs parents (Khan and Walters 1997). Pourtant, la notion d'apprentissage fut démontrée chez la Fauvette des Seychelles (*Acrocephalus sechellensis*) (Korndeur 1996) chez qui les assistants préfèrent nourrir les oisillons qui leurs sont apparentés (Komdeur 1994). L'apprentissage est spécifique et probablement lié au nombre d'évènements formateurs.

Un autre aspect de notre étude concerne la réponse au stimulus que sous-tend l'approvisionnement des oisillons. Il a été montré que les assistants répondent, de la même manière que les parents, aux variations des efforts de quête des oisillons (Wright 1998). Toutefois, il arrive que des assistants feignent de nourrir un oisillon et

gardent pour eux la nourriture (McDonald et al. 2007). Chez le Corbicrave leucoptère (*Corax melanorhamphos*), on a déterminé que ce faux-nourrissage est plus fréquent chez les jeunes assistants et qu'il est presque éliminé lorsque les contraintes alimentaires sont réduites(Boland et al. 1997).

L'Araçari vert, une espèce cavicole

La présente étude porte sur l'Araçari vert (*Pteroglossus viridis*), un ramphastidé d'Amérique du Sud qui n'est pas encore reconnu comme une espèce coopérative durant sa reproduction. La répartition de l'Araçari vert s'étend du Venezuela à la Guyane française et jusqu'à la frontière nord du Brésil. L'espèce fréquente les forêts humides de basse altitude où elle se nourrit de fruits (Remsen et al. 1993). C'est une espèce cavicole qui utilise de façon quotidienne une cavité pour le gîte et la reproduction. On connaît peu la reproduction de cette espèce en milieu naturel, si ce n'est que la saison de reproduction se déroule d'avril à juin. Les informations récoltées en captivité indiquent une durée d'incubation de 16 jours et une présence des oisillons au nid de 45 jours avant l'envol (Short and Horne 2001). Les deux parents participent au nourrissage des oisillons et ce, même plusieurs semaines après leur sortie du nid. Il existe une seule mention d'un couple qui se serait reproduit en captivité et en présence d'assistants, mais nous n'avons aucun détail sur les comportements des individus (Lindholm, données non publiées).

Plusieurs observations d'araçaris confirment la présence d'assistants sur les territoires parentaux plusieurs mois après leur envol. Les individus d'une même cellule familiale fréquentent un gîte commun pour y passer la nuit (Skutch 1958, delHoyo et al. 2002). Les habitats propices à la reproduction des espèces coopératives sont souvent saturés et défendus agressivement, ce qui suggère que la disponibilité d'un nouveau territoire puisse être une ressource limitative qui prévient la dispersion des jeunes (Emlen 1982b, Kesler et al. 2007). Parmi ces ressources limitatives, on note, chez les espèces cavicoles, la disponibilité des cavités (Walters

et al. 1992a, Newton 1994). La plupart des toucans qui utilisent des cavités pour nicher et gîter la nuit ne sont pas capables de les creuser eux-mêmes (Short and Horne 2001, delHoyo et al. 2002). Lors de la reproduction, l'alimentation des oisillons par plus de deux individus n'a été signalée que chez trois des 41 espèces de ramphastidae : l'Araçari à collier (*Pteroglossus torquatus)* et l'Araçari de Frantzius (*Pteroglossus frantzii*) (Skutch 1958, Ligon and Burt 2004) et l'Aracari à bec clair (*Pteroglossus erythropygius*) (Berg 2001).

Plusieurs institutions zoologiques et éleveurs privés reproduisent l'Araçari vert (ISIS 2009). Les efforts de reproduction ont comme objectif principal d'assurer une diversité génétique de la population captive à l'échelle de l'Amérique du Nord. Jusqu'ici, aucune étude comportementale n'a été entreprise pour documenter un aspect particulier de l'histoire naturelle de cette espèce, soit la participation des juvéniles dans l'élevage d'une nichée issue de leurs parents.

Nous croyons que cette espèce, ainsi que plusieurs autres oiseaux cavicoles non excavateurs pourraient s'adonner à une reproduction coopérative lorsque la disponibilité des cavités est faible : ne permettant pas aux juvéniles de se disperser. Ce comportement plastique serait favorisé par les pressions environnementales comme la disponibilité des sites de gîtes et de reproduction (Walters et al. 1992a, Kokko and Lundberg 2001) mais également par les bénéfices adaptatifs que peuvent en retirer les parents et les assistants (Korndeur 1996, Cockburn 1998, Heinsohn 2004). La dispersion différée observé chez les ramphastidés pourrait être maintenu par un mécanisme de leg du territoire. Toutefois, la longévité élevée chez cette famille d'oiseaux qui peut excéder la durée d'utilisation des cavités en milieu tropical pourrait limiter l'importance de ce mécanisme.

Problématique d'une reproduction coopérative en captivité

La présence des juvéniles sur le territoire parental soulève la question de la coopération dès que les parents débutent une séquence de reproduction. Les juvéniles qui ont retardé leur dispersion se retrouvent alors devant un choix : coopérer à la reproduction des parents ou demeurer sur le territoire parental sans contribuer (Ekman et al. 2004). La présence de juvéniles sur le territoire parental n'engendre pas nécessairement la mise en place de la coopération à la reproduction.

Les travaux de recherche menés sur la reproduction coopérative se sont principalement attardés aux bénéfices que peuvent en retirer les parents et les assistants. Les mesures ont surtout porté sur le succès reproducteur (Reyer 1980, Sydeman 1989, Eguchi et al. 2002), la nature des liens familiaux (Komdeur 1994, Zahavi 1995, Russell and Hatchwell 2001, Foster et al. 2006) et la structure ou la disponibilité des territoires (Woolfenden and Fitzpatrick 1984, Ekman et al. 2001b, Kesler et al. 2007). Ces études ont mis l'accent sur les résultats de la coopération et non sur la documentation des interactions comportementales entre les individus coopératifs au cours des différentes étapes de la reproduction. Il est important de mesurer les variations dans l'investissement en soins apportés aux oisillons par les individus coopérants en fonction du temps afin de nous renseigner sur le rôle de chaque individu ainsi que sur la nature des bénéfices (direct/indirect) qu'ils peuvent en retirer.

Pour documenter le comportement des juvéniles lors d'une reproduction de leur parent, nous avons offert à une famille d'Araçari vert plusieurs cavités adéquates pour le gîte et la reproduction dans un environnement artificiel qui reproduit une forêt tropicale humide comprenant de véritables arbres et arbustes. Cette étude s'est déroulée en abondance de nourriture et en absence de prédateurs dans la volière tropicale du Biodôme de Montréal. En contrôlant ces facteurs, nous étions en mesure de quantifier l'effort investi par chaque individu dans toutes les étapes de la

reproduction, particulièrement la participation des juvéniles à l'alimentation d'oisillons produit par leurs parents.

Il est reconnu *a priori* que la disponibilité des cavités qu'utilise l'Araçari vert pour la nidification et pour le gîte nocturne est un facteur qui limite la dispersion des juvéniles. Cette ressource serait limitative parce que l'espèce est un utilisateur secondaire de cavités même si un travail d'aménagement est nécessaire avant la reproduction (Short and Horne 2001, delHoyo et al. 2002). En milieu tropical on constate 2,5 fois plus de nicheurs en cavité pour environ le même nombre d'excavateurs primaires retrouvés en forêt tempérée (Gibbs et al. 1993). On remarque toutefois que peu de cavités seraient excavées par des oiseaux (0-30%) pour ensuite être utilisée par des cavicoles secondaires (Cornelius et al. 2008). Les limitations associées à la disponibilité des sites de nidification des espèces cavicoles pourraient néanmoins être sévères aux latitudes tropicales (Gibbs et al. 1993) et probablement liées à l'abondance d'autres espèces cavicoles présentes dans la communauté (Cockle et al. 2008). La faible disponibilité des cavités et la difficulté à en excaver une seraient des contraintes facilitant la consolidation des liens familiaux et pourraient favoriser l'expression des comportements coopératifs chez l'Araçari vert.

La présente étude se distingue par son cadre expérimental. La situation unique dans laquelle nous avons placé les individus est difficile à réaliser en nature. L'intérêt est de vérifier l'expression des comportements coopératifs en réduisant les contraintes environnementales liées à la disponibilité des cavités. Il est reconnu que la coopération à la reproduction n'est pas liée à un seul facteur, mais à deux processus : la facilitation écologique (faible disponibilité des cavités) et la prédisposition de l'espèce à adopter un comportement coopératif (histoire naturelle de l'espèce) (Arnold and Owens 1999). Ainsi en augmentant expérimentalement le nombre de cavités tout en maintenant les juvéniles sur le territoire parental, nous serons en mesure de tester l'hypothèse de prédisposition (importance de l'expression des traits d'histoire naturelle) chez l'Araçari vert.

Le but de cette étude est de comparer les différences comportementales entre les membres d'une famille en période de reproduction. Les observations sont faites en continu et permettent de faire ressortir la modification des comportements selon la progression de la reproduction. Nous mettons en évidence l'importance des traits d'histoire naturelle de l'espèce dans l'expression des comportements coopératifs en contrôlant les facteurs environnementaux considérés favorables à leur expression. Ainsi, nous décrirons comment l'Araçari vert peut être considéré comme une espèce coopérative dans l'élevage des oisillons même si ce comportement est facultatif à la survie de l'espèce.

Objectifs de l'étude

Cette étude vise à décrire, pour la première fois, les comportements coopératifs observés chez l'Araçari vert. Le travail qui suit est divisé en deux chapitres afin de bien cerner tous les aspects de la recherche.

Le premier chapitre porte sur l'analyse des comportements associés à la reproduction. Nous avons comparé l'investissement de chaque individu pour des comportements précis tel que l'aménagement et l'entretien du nichoir, le taux d'efficacité lors des transferts de nourriture ainsi que le nombre et la durée des visites. Cette analyse des comportements secondaires permettra d'associer un rôle aux individus ayant participé à la reproduction du couple focal. Ce chapitre se veut descriptif et permet de documenter des comportements spécifiques jamais décrits pour l'Araçari vert. Une meilleure connaissance des comportements de toucans en captivité est nécessaire dans la cadre d'une gestion conjointe de ce groupe taxinomique par les institutions zoologiques nord-américaines (Willis and Bragin 2004).

Le second chapitre porte sur la comparaison des comportements d'approvisionnement alimentaire des oisillons par les membres d'une famille d'Araçari vert. Dans notre cadre expérimental, les comportements coopératifs nous renseignent sur la nature des processus en cause (traits d'histoire naturelle vs. contraintes environnementales). L'analyse des données recueillies permet plus spécifiquement de vérifier si tous les membres de la famille ont des comportements d'approvisionnent similaires. Pour tester cette hypothèse nous avons comparé la fréquence d'alimentation des oisillons par la femelle, le mâle et les trois assistants. Les variations dans l'approvisionnement des oisillons devraient augmenter en fonction de l'âge de ceux-ci. Lors de la croissance des 25 premiers jours les besoins alimentaires des oisillons sont grandissants d'où une augmentation de l'approvisionnement global. L'intensité des comportements devrait varier selon les individus puisque chacun est différent au niveau de ses capacités physiques, de ses expériences en soin aux oisillons, du rang occupé dans la cellule familiale ainsi que du rôle tenu dans le processus de reproduction.

QUANTITATIVE ASSESSMENT OF COOPERATIVE BREEDING BEHAVIOUR OF THE GREEN ARACARI (*PTEROGLOSSUS VIRIDIS*), A CAVITY NESTER, IN CAPTIVITY

Jean-Philippe GAGNON[1,3], Pierre DRAPEAU[1], Frédérique DUBOIS[2], Serge PARENT[3]

[1] *Département des sciences biologiques, Université du Québec à Montréal, CP 8888, succ. Centre ville, Montréal, Québec, Canada, H3C 3P8;*

[2] *Département de sciences biologique, Université de Montréal,* C.P. 6128, succ. Centre-ville, Montréal, Québec, Canada, H2V 2S9;

[3] *Biodôme de Montréal, 4777 Pierre de Coubertin, Montréal, Québec, H1V 1B3*

Abstract: Since Alexander Skutch observed more than two adults entering a nesting hole of the Collared Aracari in 1958, very little has been published on the cooperative behaviour of aracaris. Two more species have been added to the list but the participation of helpers to the different tasks within the breeding cycle has never been quantitatively measured. During two breeding events, in consecutive years, we followed the breeding behaviour of the Green Aracari in a controlled environment, at the Biodôme de Montréal using an infrared camera system that allowed quantitative assessment of the behaviour of adults and helpers within a nest box. We calculated visiting rates, the time spent for cavity preparation, cleaning, incubation, and nestling feeding rates. Cavity preparation and cleaning was measured by the number of substrate transfer done by an individual. We found that preparation of the nest box prior to egg laying was mainly done by the female (2008: 67.5%, 2009: 85.2%) while incubation was shared by the parents (2008: ♀ = 41.0%, ♂ = 58.4%; 2009: ♀ = 46.5%, ♂ = 53.2%). Cleaning the nest box was done almost exclusively by the female. The number of visits was negatively correlated with their duration, except for the male where the visits were less frequent when they were short. Visit duration significantly decreased with nestling growth periods. The proportion of visits with provisioning was the highest for the female (2008: 95.5%, 2009: 98.7%) whereas the male participation to nestling provisioning was marginal. Moreover the male failed to deliver provisions (2008: 17.4%, 2009 : 16.3%) and visited without provision (2008: 34.4%, 2009 : 33:7%) more often than the female or the helpers. The helpers' contribution declined as a function of the age of nestlings. Overall, the female was the main provider in every aspect of the breeding cycle of this species.

Keywords: Cooperative, breeding, behaviour, aracari, helper, provisioning, nest cleaning, visit durations.

Introduction

The participation of helpers in cooperative breeding birds has been studied for many years in different species (Brown 1987, Koenig and Dickinson 2004). Long term behavioural and ecological studies set the theoretical foundation of this field of biology (Woolfenden and Fitzpatrick 1984, Lennartz et al. 1987, Walters et al. 1988). The overall helper effect has been studied in terms of number of helpers (Stacey and Ligon 1991), fitness variations (Buston 2004, Dickinson and Hatchwell 2004, Cockburn et al. 2008), task partitioning or provisioning adjustments (Wright and Dingemanse 1999, Canestrari et al. 2008, Ridley and Raihani 2008, Lloyd et al. 2009). Because it is difficult to monitor behaviour inside a tree hole or a nest box, few studies were conducted on cavity nesters in the wild (Lennartz et al. 1987, Ligon et al. 1988, Restrepo and Mondragòn 1998).

For secondary cavity nesters, the availability of suitable nesting holes is often an ecological constraint that may promote the expression of cooperative breeding (Emlen 1982a). Among studies on cooperative breeding, there is a lack of information on secondary cavity nesters such as toucans (ramphastids). Cooperative breeding has been proposed for three species of aracaris (*P. torquatus, P. frantzii, P. erythropygius*) by the observation, in the wild, of more than two adults visiting the same breeding cavity (Skutch 1958, Berg 2001, Koenig and Dickinson 2004). Most of the knowledge on breeding behaviour of ramphastids have been gathered in captivity, in zoos and private breeders (delHoyo et al. 2002), through the breeding of isolated pairs. Zoological institutions rarely exhibit toucans in family groups. We thus, lack information about these birds' social behaviours that are almost impossible to assess in the wild. Therefore it is important to use captive specimens to provide baseline data in this research field. To our knowledge, this study is the first to provide a quantitative assessment of the cooperative breeding behaviour of a Green Aracari family in captivity.

Helpers may assist their parents in many ways throughout the breeding cycle: nest preparation, incubation and nestling feeding. Time sharing of the nestlings care in cooperative settings implies different tasks or roles played by each member of the family. In this paper, we measured and compared how the female, the male and three helpers have invested in different behaviours related to the care of the nestlings during two breeding events.

We discuss how captive breeding programs and general welfare in captivity may benefit from specific information on the cooperative behaviour of the Green Araçari, particularly with regards to , the Piciformes taxon advisory group (TAG)

Methods

Study species

The Green Aracari is a small (30 cm, long) ramphastid found in the tropical lowland forests of Venezuela, Surinam and northern Brazil. Very little is known about the behaviour of this species in the wild. It breeds between April and June, the incubation lasts 16 days and the nestlings remain in the nest for 45 days where they are fed by both parents (Short and Horne 2001). The presence of juvenile aracaris on parental territory is confirmed for that species. Family members often share a communal roosting site located in a tree cavity (Skutch 1958) which can be used as a nesting site. As for most toucans, the Green Aracari is unable to excavate a nesting cavity (delHoyo et al. 2002) and falls into the category of secondary cavity user.

Experimental conditions

The experiment took place at the Montreal Biodôme, in a 2600 m² representation of the South American Tropical Forest. Air temperature ranges from 25 to 28°C during the day and 21 to 22°C at night. Relative humidity is at least 70%. Artificial lighting ensures a photoperiod of 14:10 in summer gradually shifting to 13:11 in winter.

Various growth stages of the tropical forest are exhibited, each with the appropriate flora (trees, shrubs, palms, herbaceous plants): the mature forest, the secondary forest and the flooded forest. The fauna includes mammals, reptiles, amphibians, fishes and 50 to 60 free flying birds representing 20 to 30 species. The Green Aracari is a passive (non-aggressive) dominant bird at feeders. In November 2007, a breeding pair was formed by introducing a 7 year old female with the resident 13 year old male. A first reproduction successfully occurred in February 2008, producing three females who then became helpers later in 2008 and in 2009.

During the breeding periods, four cavities were available to the aracaris. Two were wooden nest boxes, designed according to the recommended AZA specifications (Seibels and Vince 2001) located 8 meters apart. Those nesting cavity were filled with a 5 to 10 cm layer of wood chips. The third cavity was a circular PVC box (40 cm diameter X 50 cm) only used for roosting. The other cavity was an artificial exhibit element in the shape of an 18 m. deep tube with a 20 cm opening at the top. The aracaris only used the first few centimetres of this tube as roosting site for the night. After visiting all cavities (n=4), the female chose one as the nesting site.

The first breeding event occurred in 2008 where the first of a two egg clutch was laid on July 27. When the young fledged they were removed form the aviary (October 2008). All nest boxes were also removed to prevent unwanted breeding. The two remaining cavities (the PVC box and the "tube") were used on a regular basis for roosting. In 2009 the first of a three eggs clutch was laid on June 1. Data collection was ended after all nestlings fledged. On both years, incubation lasted 16 days and

fledglings left the nest 40 days after hatching. We were able to monitor feeding behaviour adequately from hatchling to the first 25 days inside the nest box. Past that time, nestlings started climbing the nest wall toward the entrance of the box where they were out of the camera's field of view.

Audio visual equipment

We followed two reproductive sequences of Green Aracari, on consecutive years (2008 and 2009). To insure correct identification, all individuals were leg banded with different colour and equipped with an under skin passive integrated transponder (PIT), located between the scapulars (model: 134.2 kHz, ISO). Leg bands were used for direct visual identification while PIT tags were used in conjunction with a Biomark reader (model: FS-2001) for continuous monitoring.

Following the selection of a nest box by the female, a video camera (model: WK-CIE48HVCD) was installed to record behaviour inside the nest box. The camera is equipped with 48 built-in infrared lights (LED) enabling recording in almost complete darkness without disturbing the birds (Pierce and Pobprasert 2007). In 2008, the camera system was coupled with the microchip reader attached to the nest box so as to confirm the identification of individuals when the leg band was not visible with the camera. In 2009, a second camera was installed outside the nest box for this purpose only, while the PIT reader was transferred to monitor the roosting cavity (the «tube») were all helpers spent the night.

The camera system was linked with a security software (EZCapture 7.1, Avermedia technology Inc.) for archiving video on computer files. Video capture was automated by motion detection and was effective from 6:00 to 21:00 hr. during the entire breeding period. From 21:00 to 6:00 all birds were roosting for the night and, hence, no specific care toward nestling was performed. More than 800 hours were recorded for each breeding event in 2008 and 2009. For this paper we analysed individual

behaviors for over 750 hours during each year's breeding period corresponding to the nest building, nest incubation and until the 25th day after hatching.

Breeding chronology

Over the two years of our study, nine clutches were laid (Table 1.1). The first breeding attempt (2008.1) was successful and produced the helpers that were all females. A second clutch was laid and eggs were sterilised, but kept in the nestbox to slow the egg production. Five more clutches were produced in 2008 but eggs were damaged. Eggs of clutch 3 were also sterilised and then removed and those of clutches 4-5 were ejected by the birds themselves. It was noticed that the aging male was having a hard time getting to the bottom of the nest, and it was thought that the collision with the eggs might have damaged them; leading to their ejection. Therefore the nest box was inclined at an angle of 45° on June 23 of 2008. It is difficult to link a particular event to the breaking of an egg. It may have occurred while the five individuals roosted in the nest box or for some other reason. The ejection of the damaged eggs of clutch no. 5 in 2008 was made by a juvenile. The sixth clutch in 2008 contained three eggs and one was damaged by another juvenile and ejected the same day. This was the second successful breeding, three helpers participated and it produced two nestlings. They were however, removed from the experimental unit 16 weeks after hatching. In 2009, the helpers roosted in a different cavity than the parents, the nest box was inclined and no eggs were damaged. The two first clutches of 2009 were not fertile and were removed after 18 days (2009. 1-2). The third clutch was composed of three eggs that all hatched, and two of the same helpers assisted their parents. In our analysis, we summed the contribution of all juveniles under the name "helpers". The variations observed in the behaviour of each individual reflect a response induced by the different number of nestlings.

Data collection

Four stages define the breeding cycle of Aracaris: nest preparation, egg incubation, nestling feeding and weaning. This study describes behaviour occurring inside the nest box for the first three stages of the breeding cycle. Behaviour occurring outside the nest box was not monitored.

Each year, behaviour at the nest box was quantified for the female, the male and two or three female juveniles. For every visit to the nest box, the following data were recorded: identification of the provider, time of arrival and time of departure. At the preparation stage, the number of visits where woodchips were removed was noted. During egg incubation, we calculated the time spent by an individual sitting on the eggs. At the nestling feeding stage we calculated the number of visits when woodchips were removed. We also noted when an individual gave at least one provision to a nestling, tried but failed or visited without provisioning. Data were then converted in visiting rates (number of visits per day), visit duration (in seconds), nestling feeding rates (number of provisions transferred per hour per nestling). A provision was counted each time a provider introduced its beak into a nestling's beak to transfer food. Because the food available to aracaris was in the form of softbill pellets or diced fruit, the size of every feeding was considered standardized and equivalent. We also considered the number of provisions transferred to a nestling to be accurate and representative of the feeding effort provided by an individual (Canestrari et al. 2005).

Data analysis

We compared the observations of two breeding events, occurring on successive years (2008 and 2009) to characterize the behaviour of the five members of a family group of Green Aracari.

Nest preparation

The duration of the nest preparation was set at 7 days, using the shorter inter-breeding period observed. Preparation of the nest consists in removing woodchips from the artificial nest box over a period of 7 consecutive days. Using a chi-square test, we analysed the homogeneity of woodchip removal among individuals. Proportion (%) of visits that led to woodchip removal was used to compare individual and years.

Egg incubation

The amount of time invested in incubating eggs was measured for the female, the male and the helpers in both breeding events. Eggs were laid at the rate of one per day and the incubation started with the laying of the last egg. The overall incubating period is described by the proportion of time shared (%) by individuals. We analysed the variation of the daily incubation duration based on individuals and years with a Wilcoxon rank-sum test.

Nest box maintenance

After hatching, nest maintenance involved the removal of soiled woodchips from the nest box. With a Chi-square test, we analysed the homogeneity of woodchip removal among individuals. As for nest preparation, the proportions (%) of visits that led to substrate removal were quantified.

Nestling feeding

To establish a comparative position between providers based on their relative contribution, in both years, we calculated the total number of visits and the total number of provisions given to the nestlings. A chi square test was used to analyze the homogeneity of the visit-feeding behaviour among the providers.

In order to assess the ability of individuals to feed nestlings, the number of visits to the nest by a given bird were calculated as follows: the number of visits who ended with at least one provision transferred, the number of visits where the provider failed to deliver a provision and the number of visits where the provider came to the nest box without provision. A Chi-square test was used to test homogeneity in the visits among the female, the male and the helpers.

Visits (frequency and duration)

The non-parametric Kendall's tau measure of correlation was used to evaluate the link between the number and the duration of the visits. The duration of a visit varied with the feeding individual and the nestlings' age (days).

Variation of visit duration was also compared as a function of the metabolic changes observed in the growing nestlings. To compare trends between cooperative individuals, we pooled data into three periods to cover different nestling stages. The first period extended from egg hatching to the appearance of feathers on the nestlings' wings (day 1 to 8). The second period was established from the appearance of feathers to the opening of the nestlings' eyes (day 9 to 20). And the last period from the eyes opening to the moment nestlings start climbing towards the nest box entrance (day 21-25). We used a Kruskal-Wallis test or a Wilcoxon rank-sum test, to test the statistical hypothesis of homogeneity of visits duration between years, periods and individuals.

Results

Nest preparation

The total number of visits during this period differed between years (2008: 258, 2009: 228), but the proportion of woodchip transfers (2008: 166, 2009: 162) was not significantly different (X^2=0.481, df=1, p= 0.4880). The female (2008: 67.5%, 2009: 85.2%) made significantly more woodchip transfers (2008: X^2=28.444, df =1, p< 0.0001*; 2009: X^2=65.801, df=1, p< 0.0001*) than the male (2008: 32.5%, 2009: 14.8%). Even when juveniles visited the nest box during this period (2008= 15, 2009= 6), they never took out woodchips (Figure 1.1).

Egg incubation

Incubation lasted 16 days in both years. The male and the female shared the incubation during the day. Helpers visited the nest box, but on only one occasion in 2008 did a helper sit on the eggs for few seconds. Because at least two birds communally roosted in the nest box, it was impossible to determine which one incubated the eggs during the night. The proportion of daily total duration (minutes) spent incubating by the female was 41.3% and 58.7% for the male in 2008, and 46.7% by the female and 53.3% by the male in 2009. When comparing years, we found a significant variation in the daily total incubating duration for the female (Z=3.1015, p=0.0019*) but not for the male (Z= -0.2571, p=0.8005). In 2008, the daily total incubating duration was significantly different between the male and the female (Z=3.0096, p = 0.0026*) but no significant difference, was found in 2009 (Z=1.7230, p=0.0849) (Figure 1.2).

Roosting in the nest box was done by all individuals until the nestlings were 4 days old in 2008. Thereafter, the helpers adopted another roosting site until the end of the project in August 2009.

Nest box maintenance

Few days after hatching nestling dejections began to soil the substrate inside the nest box. Woodchip removal started on day 6 in 2008 and on day 4 in 2009. The female made 95.2% of the cleaning behaviour in 2008 and 97.1% in 2009. The male accounted for 2.5% of the cleaning in 2008 and 1.6% in 2009. The helpers did 2.3% of the cleaning in 2008 and 1.3% in 2009. The female did significantly more visits with cleaning behaviour (2008: X^2=779.765, df=2, p<0.0001*; 2009: X^2=603.750, df=2, p<0.0001*) (Figure 1.3).

Nestling feeding

In 2008, the five members of the family made a total of 1521 visits (female: 781, male: 247, helpers: 493) to the two nestlings and brought at the nest 2946 provisions (female: 2110, male: 145, helpers: 691; to the two nestlings). In 2009, four members of the family (one juvenile did not help) made 1792 visits (female: 1113, male: 202, helpers: 477) for a total of 4994 provisions (female: 3972, male: 126, helpers: 896). Chi-square tests of homogeneity showed that only the visits/provisions totals of the male were similar between years (Table 1.2).

When an individual visited the nest box during the provisioning period, three different events occurred: feeding at least one nestling, visiting the nest with a provision but failing to deliver it, or visiting the nest without provision (Figure 1.4). The Chi-square test of homogeneity of feeding visits was rejected between individuals (2008:

X^2=379.684, df=4, p<0.0001*; 2009: X^2=617.001, df=4, p<0.0001*). The female and the helpers did more visits that lead to nestlings' provisioning than they failed to deliver provision or visited nests without provisioning. The male failed to deliver provisions to at least one nestling in 43 of 247 visits (17.4%) in 2008, and in 33 of 202 visits in 2009 (16.3%). He also visited the nest box 85 times (34.4%) with no provision in 2008, and 68 times (33.7%) in 2009. The number of visits with provisioning that were made by the female reflected the different number of nestlings (353 more visits with provisioning were done when three nestlings were in the nest box). This was not the case, however, for the male and the helpers (X^2=1.599, df=1, p=0.2060). Based on the total number of provisions, the female gave significantly more provisions to the nestlings than did the male and the helpers (2008: X^2=2095.35, df=2, p<0.0001; 2009:X^2=4975.249, df=2, p<0.0001) with 71.6% of all the provisions to the nestlings in 2008 and 79.6% in 2009.

Visits (frequency and duration)

The Kendall's tau test showed a significant correlation between the number of visits and their duration. This relationship was negative for both years for the female. When more visits were made to the nest box they were of shorter duration. The same trend was observed for the helpers but was statistically significant only in 2008. The male had the opposite behaviour; when fewer visit where made they were longer (Table 1.3).

Most of the visits during the nestling feeding were short and oriented towards provisioning. For each provider (female, male and helpers) the variation in visits duration was compared among three growth periods. The visit duration by the female was similar between years at periods A and B, but significantly shorter in 2008 during period C (Figure 1.5(a)). The visit duration by the male was longer in 2008 at period A, similar between years for period B and shorter in 2008 at period C (Figure 1.5(b)). Helpers did not feed any nestling in the first period of 2009, thus no statistical

analysis was performed for helpers at period A. The visit durations by helpers at period B was similar between years and the visit durations was longer in 2008 at period C (Figure 1.5(c)).

The visit duration followed a general decreasing pattern between periods for the female, the male and the helpers. Period A had the longest visit duration, followed by period B and period C (Figure 1.5). The visit duration by the male was similar between period B and C in 2009 (Figure 1.5(b)).

When comparing the visit duration between individuals, we found that the male was the one who made the longest visit in all periods in 2008 (Figure 1.6). The female made significantly longer visits than helpers in all periods and in both years (Figure 1.6). The visit duration by the male and by the female were similar between period A and B in 2009 (Figure 1.6(a), (b)).

Discussion

Preparing the cavity before egg laying was mainly done by the female. In the early stage of the breeding season, the female explored all cavities available in the enclosure. Once she made her choice, she engaged in woodchip removal, often repeatedly for short periods of time. The male also participated to woodchip removal, but to a lower frequency i.e., for half of the visits. The helpers were seen frequently around the nest box and visited the nest box on a few occasions, but never did any woodchip removal. Helpers seemed "clueless" when entering the empty nest box during the day.

The incubation period of the Green Aracari is best described by a time sharing behaviour between the female and the male. The eggs were left alone only for very short periods of time. When not incubating the eggs, parents were seen feeding or

perched nearby the nest box, sometimes in the presence of helpers (Gagnon, pers. obs.). Even if helpers visited the nest box and showed interest in the eggs by touching them with the beak, only one helper sat on the eggs for only one short period in 2008. No agonistic behaviour was observed when helpers and an adult were together in the nest box. The significant daily variation in the incubating duration of the female observed in 2008 could be related to the successive clutches laid during that year, or to some parameters not monitored in this study.

Our observations of the nest box attendance revealed that the female was the main provider. The combined attendance of the helpers was twice that of the male which suggests a high level of interest. As it was the case for nest preparation, the cleaning maintenance was done almost entirely by the female. Even if helpers had never been inside the nest box when an adult proceeded to remove woodchip, they did it on 23 occasions (2008: 14, 2009: 9). This behaviour therefore was not learned or reproduced by imitation, but while perched nearby, the helpers may have seen a parent exiting the nest box and discarding woodchips. It is unclear why the male and helpers removed woodchips so infrequently. Similar behaviour is found on the Red-cockaded woodpecker where only one individual excavates when helpers are present in the group (Harding 1997).

The ability of feeding the nestlings was measured with regards to three different outcomes when an individual visited the nest box. Because our data were not adjusted for the number of nestlings, the results clearly show the female delivered more provisions when there was three nestlings instead of two. This is very different from the male and the helpers, who showed very little change in nestlings provisioning effort as a function of the clutch size. When an individual failed to deliver a provision to a nestling, it ate it before leaving the nest box. This means when a bird enters the cavity with food in its beak, it will not necessarily feed the nestlings. For an observer located outside the nest box this may lead to an inaccurate observation and care should be taken in similar studies on cavity nesters to avoid this type of bias, a result of indirect monitoring. The male was the worst nestling feeder for visiting the

nest box without provision, or failing to deliver provision more times than the other providers.

The duration of the visits decreased as nestlings grew. The male and the female stayed in the nest for longer visits on the first 8 days after hatching than afterwards. We propose as an interpretation that nestling Green Aracari are unable to maintain their body temperature when they are only few days old. Passerine birds complete most of their growth in body-weight before they develop strong homoiothermic capacities (Ricklefs 1976). Metabolic requirements could thus be associated with longer visits and the "incubating" position adopted by the visiting individual when staying inside the nest box during that period. The nestlings are born naked and blind. Their feathers start piercing the skin at day 9. The visit duration of the male and the female shortened on the second period of growth, then the number of visits made by the female increased and the helpers began visiting the nest box regularly. A negative correlation between the number and the duration of visits was observed for the male. His role in the breeding cycle may be associated to vigilance other than nestling provisioning. Nevertheless, the visiting-feeding patterns are similar between years for all providers and the observed change in feeding behaviour seems to correspond to the metabolic requirements of the nestlings.

The same group of helpers was artificially maintained within the experimental unit for two years. A major difference between the breeding events was that only two of the three helpers participated in nestling feeding in 2009. Because it is difficult to evaluate the benefits gained by helpers in our study, we can only say that helping behaviour appeared to have declined with time. In natural habitats older helpers should be replaced by the generation that they helped. More studies on the composition of ramphastid groups are needed to further investigate this hypothesis.

Over the nine clutches we monitored, the contribution of helpers did not always lead to a positive output. Brown (1978) separated helper behaviour in two categories, potentially beneficial or potentially harmful. The participation of helpers in critical

aspects of breeding may play against the breeders and prolong, delay or abort the production of independent fledglings. In our study, it is important to keep in mind the history of the clutch when comparing the two successful cooperative breedings. In 2008, before the hatching of clutch 2008.6 the female raised 3 juveniles, prepared a cavity 5 times and laid a total of 19 eggs. In 2009, the female prepared a cavity on 3 occasions and laid 9 eggs. Even if food is readily available, we may suppose that the level of energy of the female was not equivalent between the two events, but no measurements were taken to control this aspect. At his first breeding (2008.1), the male, 14 years old, was considered old among the captive population in North America, according to the life table of the captive population management plan of the species (Willis and Bragin 2004). His low level of participation might be associated with his age, but the duration of the visits made among the different periods of the breeding suggests otherwise. The male's presence in, or in the vicinity of the nest box, might express a protection behaviour. Animals held in captive habitats are prone to express vigilance behaviour in response to a wide range of potentially provocative environmental challenges (Morgan and Tromborg 2007). When comparing breeding events, we have to keep in mind, however, that the age and health condition of the breeders and helpers might alter the expression of their behaviour. Metabolic requirements of the growing nestlings should be studied under the assumption that the provider behaviour changes with time.

There is little information on the breeding behaviour of ramphastids. Hence, any new information on their behaviour improves our understanding of their biology. Our observations revealed the importance of the family group for this species. The gregarious nature of the Green Aracari, also noted for other aracaris in the wild (delHoyo et al. 2002), emphasizes the need to keep small toucan in groups while in captivity. This could also be true for other gregarious species having social or family interactions modulate individual behaviour.

We are fully aware that our study lacks the statistical power that a large number of breeding events would have provided, but the description made on the cooperative breeding of the Green Aracari provides at least some useful indication for further

research. For instance in captive breeding the inclusion of behavioural knowledge such as cooperative breeding to task force groups such as the Piciformes taxon advisory group (TAG) may improve breeding of this species in captivity across zoological institutions. Comparisons of breeding performance between institutions with standardized sampling protocols could indeed provide the conditions in terms of sample size to reach robust conclusions on the benefits of cooperative breeding of this species.

In the wild, knowing that cooperative breeding occurs in ramphastids means that multiple cavities should be preserved in the vicinity of parent's nest. Such situation, where offsprings leave the nest but stay on parental territory, will promote delayed dispersal while stimulating breeding of the couple. More studies are needed to understand how food availability, territory turnover and cavity lifespan affect the breeding behaviour of toucans. Studies in the wild on tropical species are challenging, and behavioural studies in captivity should be considered as a useful, and sometimes the only feasible alternative.

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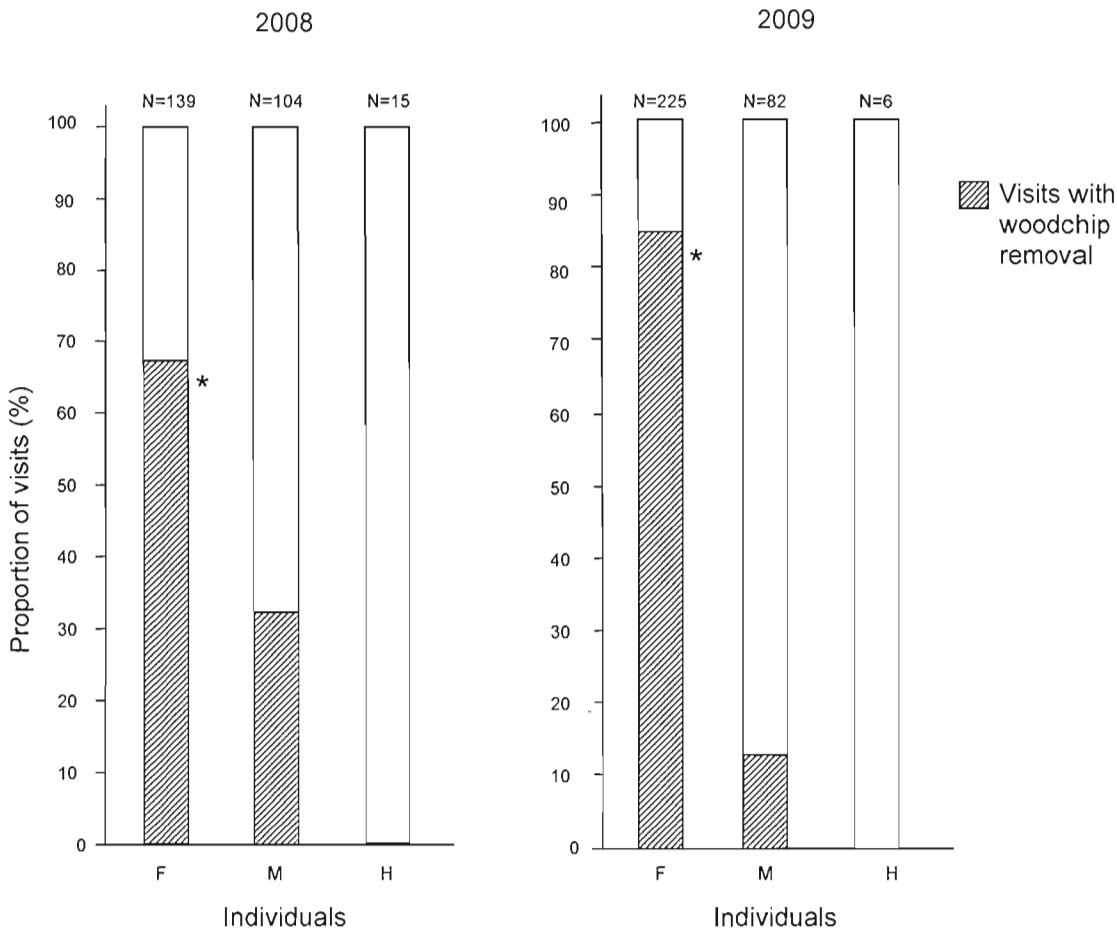

Figure 1.1 Proportion of visits with woodchip removal over 7 days prior to egg laying by individual for Green Aracari female (n=1), male (n=1) and helpers (n=3) from two breeding periods in captivity at the Montreal Biodôme. Total numbers of visits are shown on top of histograms. Asterisk (*) identify the individual who made significantly more woodchip removal visits on a given year ($p < 0.001$).

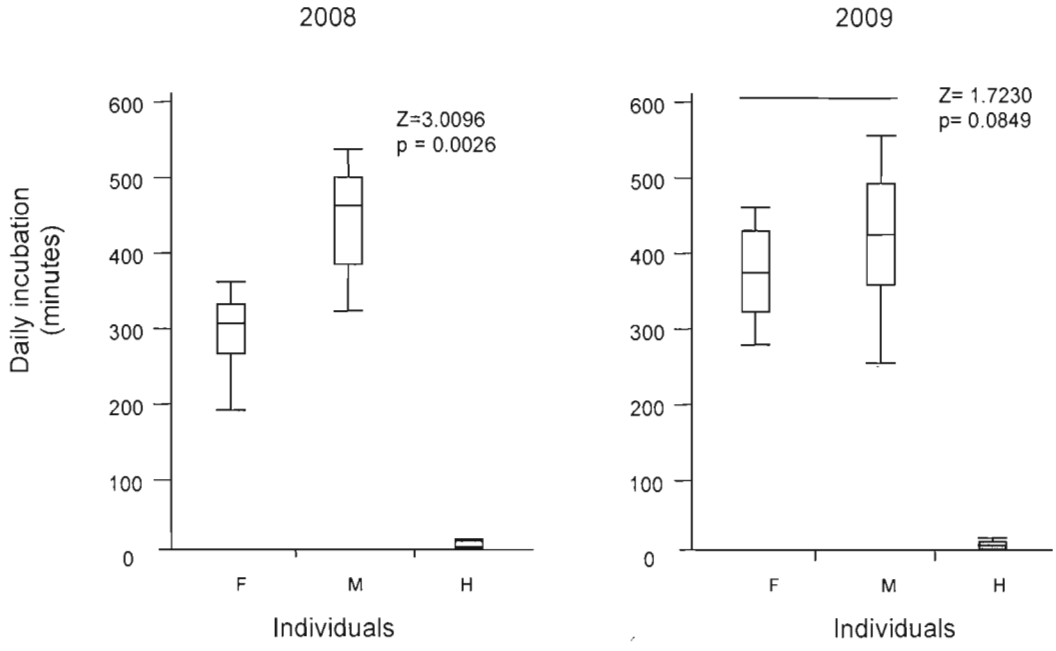

Figure 1.2 Median daily duration of Incubation over 16 days by individuals for Green Aracari female (n=1), male (n=1) and helpers (n=3) from two breeding periods in captivity at the Montreal Biodôme. Box plots show the daily variation of the duration in minutes. Solid lines show no significant variation between individuals.

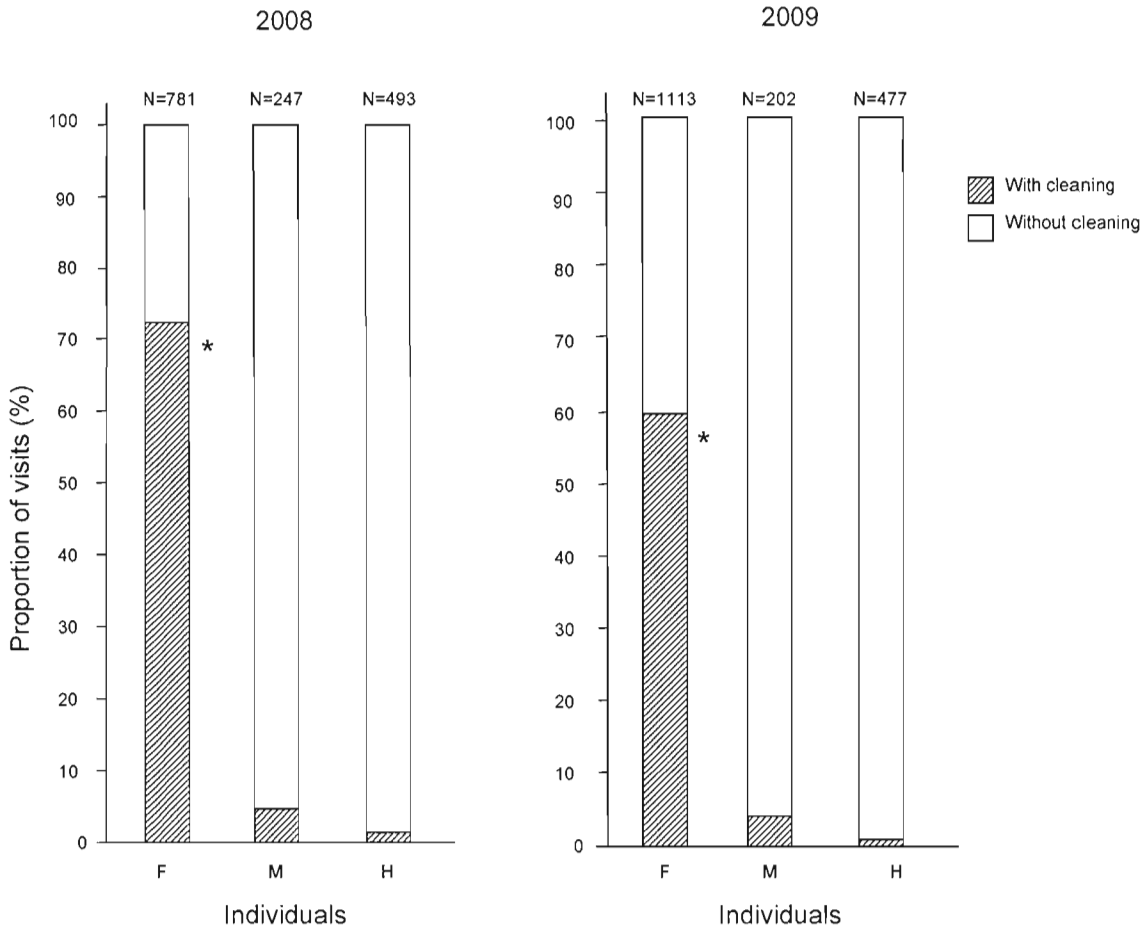

Figure 1.3 Proportion of visits with cleaning of the nest box by individual for Green Aracari female (n=1), male (n=1) and helpers (n=3) from two breeding periods in captivity at the Montreal Biodôme Total numbers of visits are shown on top of histograms. Asterisks (*) identifies the individual who made significantly more visits for woodchips removal for a given year ($p < 0.001$).

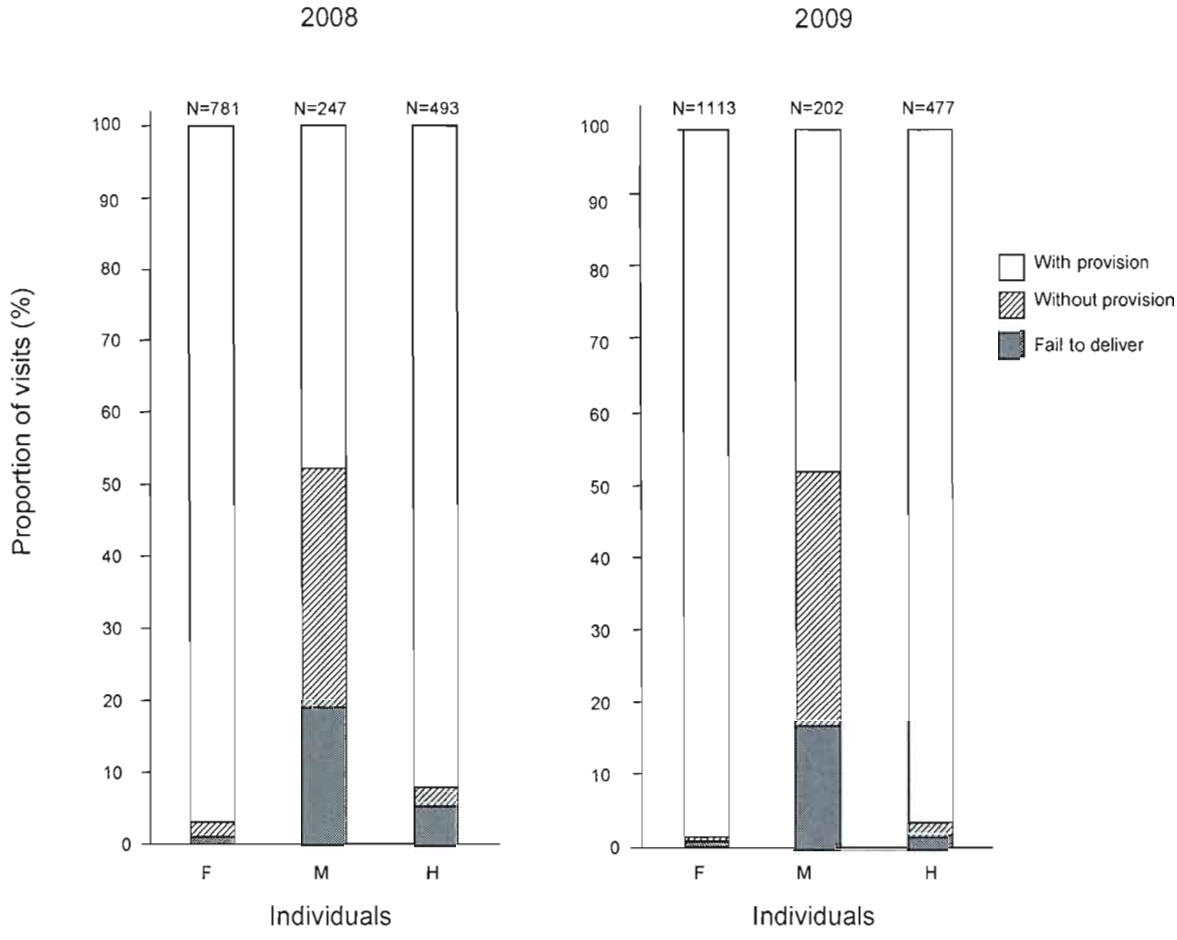

Figure 1.4 Proportion of visits by provisioning issues and individual for Green Aracari female (n=1), male (n=1) and helpers (n=3) from two breeding periods in captivity at the Montreal Biodôme. Histograms represent a successful provisioning (clear), a fail delivery (gray) and visits without provisioning (dashed). The total numbers of visits are shown on top of histograms.

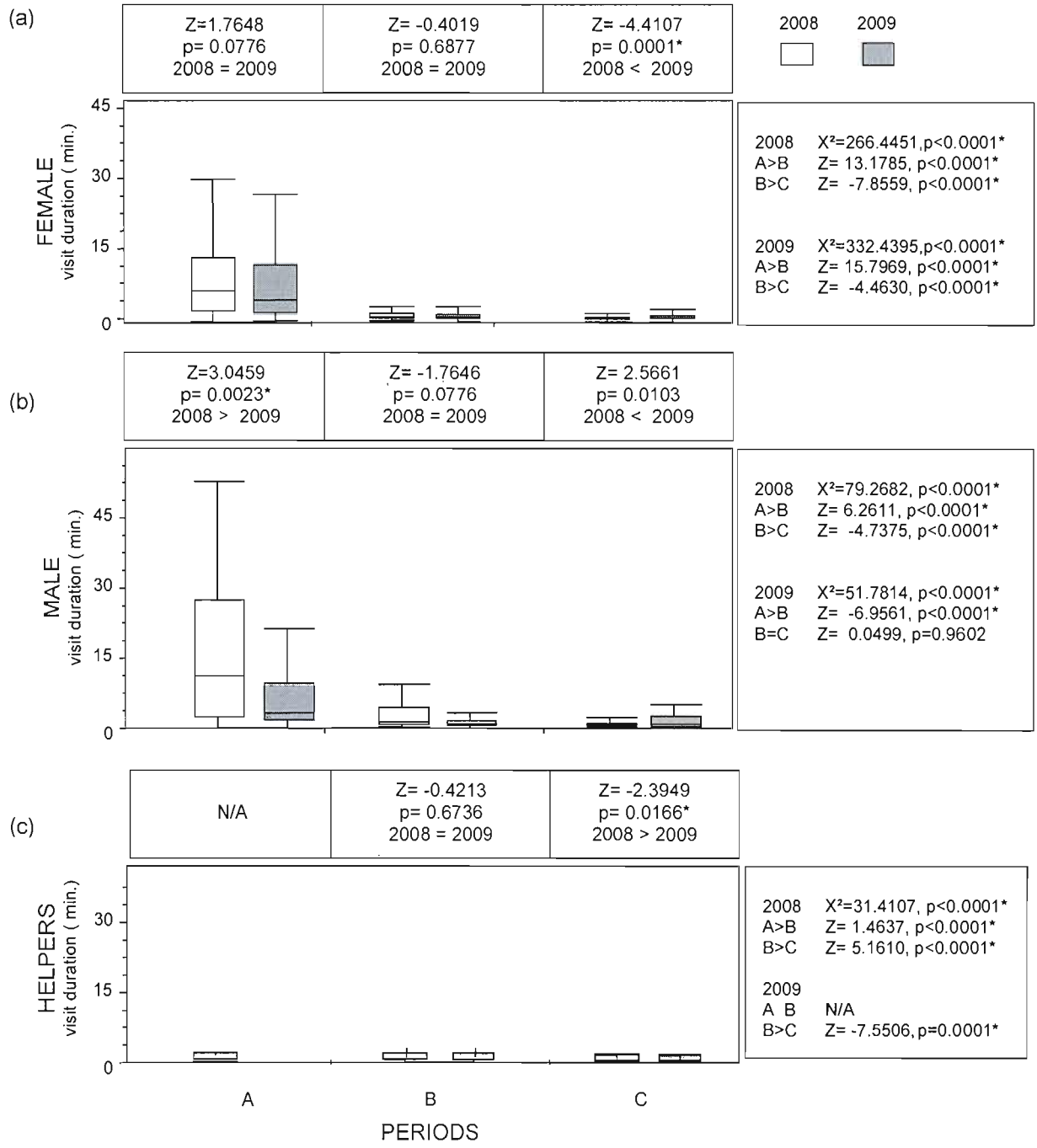

Figure 1.5 Variation of visit duration by nestling growth periods and years for Green Aracari female (n=1), male (n=1) and helpers (n=3) from two breeding periods in captivity at the Montreal Biodôme. Box plots are quantiles of visits duration calculated in minutes and pooled in periods for the female, the male and helpers in 2008 and 2009.

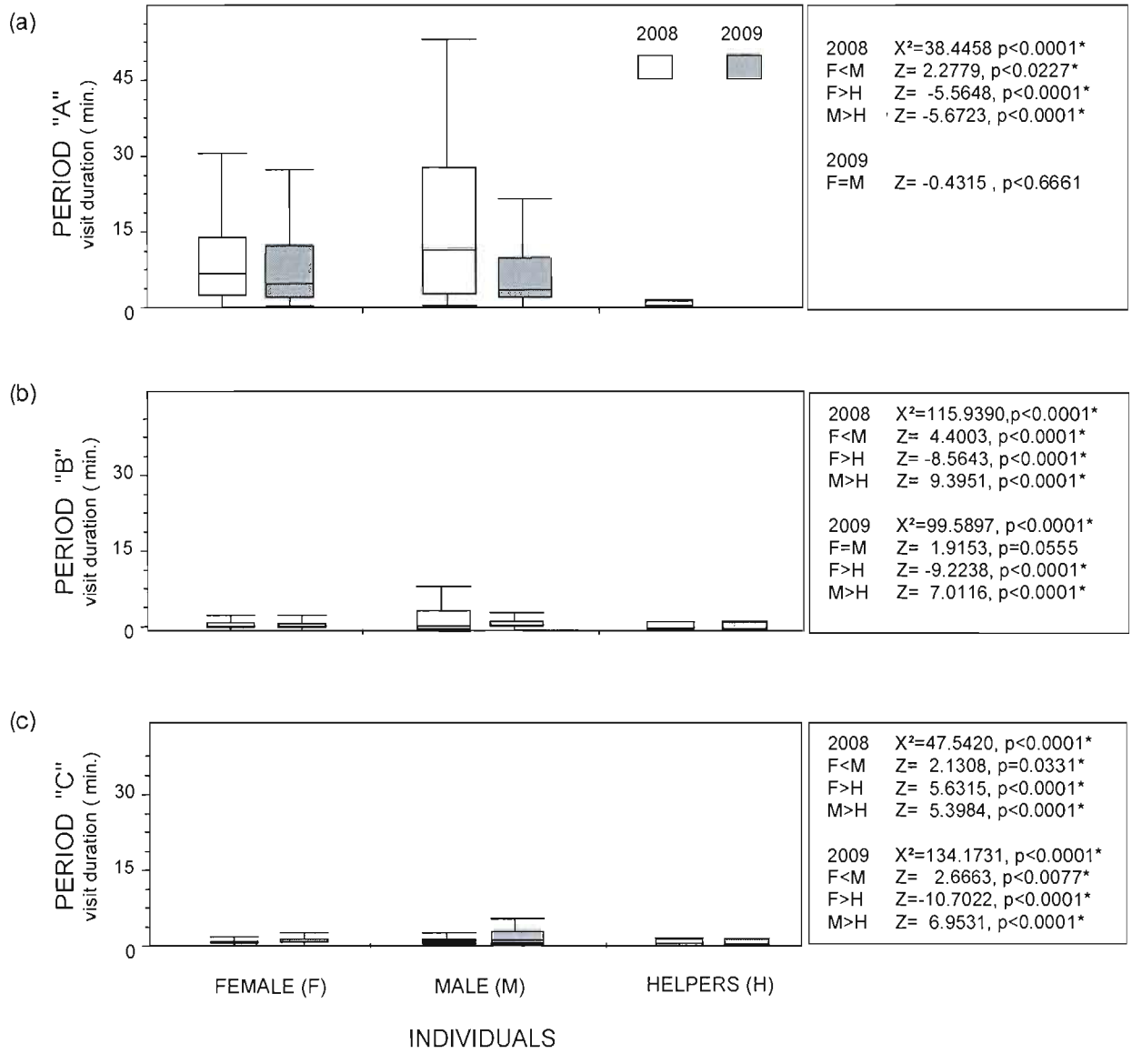

Figure 1.6 Variation of visits duration by individuals and years for Green Aracari female (n=1), male (n=1) and helpers (n=3) from two breeding periods in captivity at the Montreal Biodôme. Box plots are quantiles of visits duration calculated in minutes and pooled in periods for the female, the male and helpers in 2008 and 2009.

Clutch #	First egg laid	Hatching	Fledging	End of clutch	Notes
2008.1	25-12-2007	11-01-2008	22-02-2008		Helpers (3 females)
2008.2	30-03-2008	•	•	05-03-2008	eggs sterilised
2008.3	21-04-2008	•	•	27-04-2008	eggs sterilised
2008.4	02-06-2008	•	•	14-06-2008	eggs ejected
2008.5	01-07-2008	•	•	17-07-2008	eggs ejected
2008.6	27-07-2008	12-08-2008	21-09-2008		2 chicks
2009.1	15-04-2009	•	•	05-05-2009	eggs removed
2009.2	15-05-2009	•	•	22-05-2009	eggs removed
2009.3	01-06-2009	17-06-2009	27-07-2009		3 chicks

Table 1.1 Clutch chronology of a captive Green Araçari breeding pair (n=1) at the Montréal Biodôme in 2008-2009. Helpers (n=3) were kept in the aviary with breeding pair at all time from hatching to December 2009.

Behaviour	Years	F	M	H	TOTAL	X^2	Prob.
# visits	2008	781	247	493	1521	281.799	<0.0001*
	2009	1113	202	477	1792	731.05	<0.0001*
# provisions	2008	2110	145	691	2946	2095.35	<0.0001*
	2009	3972	126	896	4994	4975.249	<0.0001*
X^2		26.756	0.154	12.845			
Prob.		<0.0001*	0.6947	<0.0001*			

Table 1.2 Homogeneity test of the total number of visits and number of provisions by individuals for Green Aracari female (n=1), male (n=1) and helpers (n=3) from two breeding periods in captivity at the Montreal Biodôme. Chi square values and probability tested for homogeneity by individuals (df = 2) and years (df=1). F=female, M=male, H=helpers.

Year	Individual	t	Prob.
2008	Female	-0.1227	< 0.0001*
	Male	0.1702	0.0064*
	Helpers (3)	-0.1525	< 0.0001*
2009	Female	-0.2011	< 0.0001*
	Male	0.1662	0.0130*
	Helpers (2)	-0.0304	0.4057

Table 1.3 Kendall tau correlation between the number and the duration of visits for Green Aracari female (n=1), male (n=1) and helpers (n=3) from two breeding periods in captivity at the Montreal Biodôme. Data range from hatching to day 25 of each breeding events.

HIGH CAVITY AVAILABILITY DOES NOT PREVENT COOPERATIVE BREEDING OF A GREEN ARACARI *(PTEROGLOSSUS VIRIDIS)* FAMILY, IN CAPTIVITY

Jean-Philippe GAGNON[1,3], Pierre DRAPEAU[1], Frédérique DUBOIS[2], Serge PARENT[3]

[1] *Département des sciences biologiques, Université du Québec à Montréal, CP 8888, succ. Centre ville, Montréal, Québec, Canada, H3C 3P8;*

[2] *Département de sciences biologiques, Université de Montréal,* C.P. 6128, succ. Centre-ville, Montréal, Québec, Canada, H2V 2S9;

[3] *Biodôme de Montréal, 4777 Pierre-de-Coubertin, Montréal, Québec, H1V 1B3*

Abstract: Cooperative breeding is rare in bird species. Generally, helpers are juveniles who have delayed their dispersal and stay on the parental territory. For small toucans such as aracaris, the availability of cavities for nesting and roosting is one of the major ecological constraints that lead to delayed dispersal. In a controlled environment, at the Biodôme de Montréal, three juveniles were maintained with their parents while four cavities were available. The high availability of cavities was expected to weaken the family bonds or reduce helping behaviour. Using an infrared surveillance camera inside the nest box we monitored the nestling-feeding rates of a Green Aracari family for two consecutive breeding events (2008, 2009). The family cell was composed of a female, a male and three juveniles who acted as helpers. The female provided most of the nestling provisioning (2008: 71.6%, 2009:79.5%). The nestling provisioning by the male was less than 5% at each year. The nestling feeding rate by the helpers (N_{2008}=3, N_{2009}=2) varied accordingly to the female's feeding rate. An increasing nestling-feeding rate is positively correlated with the age of the nestlings with daily feeding peaks between 6:00 and 8:00, and between 16:00 and 18:00. Comparison between years showed no significant variation in the nestling-feeding rate by the female, while the male and helpers lowered their rates in 2009. Because no variation was observed in the nestling feeding rates of the main provider, help should not be considered compensatory. In our controlled environment increasing the cavity availability, which is considered a limiting factor in juvenile dispersion, did not prevent the expression of cooperative behaviour indicating that such behaviour is linked to the life history traits of the species, whereas ecological constraints modulate their expression.

Keywords: Cooperative breeding, ecological constraint, toucan, aracari, nestling feeding.

Introduction

The majority of cooperative breeders exhibit delayed dispersal of offsprings, which subsequently forego reproduction and become non-reproductive helpers at the nest of parents or close relatives (Ekman et al. 2004). Dispersal may be delayed under ecological constraints, such as low habitat productivity or saturation, nesting site availability, or access to a mate (Emlen 1982a, Walters et al. 1992b, Emlen 1995, Arnold and Owens 1999, Russell 2001, Kesler et al. 2007). For cavity nesters, availability of suitable holes for roosting and nesting is a critical resource that leads to delayed dispersal and cooperative breeding (Walters et al. 1988, Newton 1994).

When dispersal is delayed, benefits may arise for helpers and parents. The *philopatry* hypothesis suggests that a juvenile may gain fitness when staying on parental territory even without participating in the breeding of its parent (Stacey and Ligon 1991). When assisted, parents may improve their fitness by increasing their own survival (Khan and Walters 2002), their breeding success (Williams and Hale 2006, Blackmore and Heinsohn 2007, Doerr and Doerr 2007) or by reducing their cost of breeding (Langen 2000, Russell et al. 2007). Research about cooperative breeding has focused on many aspects of the helper-breeder relationship, such as kinship (Komdeur 1994, Wright et al. 1999), provisioning rules (Wright 1998), social structures (Reyer 1980, Gayou 1986, Lennartz et al. 1987), and nepotism (Gayou 1986, Ekman et al. 2001a). The overall helper effect has been studied in terms of number of helpers (Stacey and Ligon 1991), fitness variation (Buston 2004, Dickinson and Hatchwell 2004, Cockburn et al. 2008), task partitioning or provisioning adjustments (Wright and Dingemanse 1999, Canestrari et al. 2008, Ridley and Raihani 2008, Lloyd et al. 2009). However, the daily variation in the helpers' contribution during the breeding period has received little attention. The daily feeding pattern of helpers needs to be analysed to determine if help is provided randomly or if it follows the same provisioning profile exhibited by the parents. When adjustments

are made by the parents according to the helpers' contribution, helping behaviour could be defined as compensatory and linked to a gain in fitness.

Since Skutch (1958) reported helpers at a nest of Collared and Fiery-billed Aracari (*Pteroglossus torquatus* and *Pteroglossus frantzii*), very little has been documented on cooperative breeding in ramphastids. Sightings of at least one helper at the nest of a Pale-mandible Aracari (*Pteroglossus erythropygius*) (Berg 2001) suggests a wider occurrence of this behaviour among ramphastids than initially expected. Aracaris are known to be gregarious in their feeding habits. They roost and breed in groups in hollow trees which they cannot excavate by themselves. We thus may assume that dispersion of secondary cavity nesters, like aracaris, is limited by the availability of suitable holes. Most of them breed in pairs and only a few species are known to breed in groups of 4 or 5 individuals (delHoyo et al. 2002). Gibbs (1993) considered that with 2.5 times as many cavity nesting species and less than half as many snags than in temperate forests, limitation for cavity nesting birds could be more severe in tropical forests. Dependency on hole availability for roosting and breeding makes aracaris good candidates for behavioural studies in a controlled environment.

Cooperative breeding relies on two factors: a combination of life history predisposition and ecological facilitation (Arnold and Owens 1998). Life history traits include low mortality rate, delayed maturity, small clutch size, sedentariness, lower latitude distribution and reduced environmental fluctuation. Those two factors act in concert by influencing the rate of turnover of suitable breeding opportunities and should be viewed as a broad constraints hypothesis that incorporates both (Hatchwell and Komdeur 2000). In this paper, we monitored the behaviour of a breeding pair of Green Aracari (*Pteroglossus viridis*) in captivity. Our study was conducted in a controlled environment where food and cavities were numerous, thus reducing constraints that usually facilitate cooperative breeding. We tested the hypothesis that the life history of the species is a key driver in the expression of cooperative breeding. More specifically, we focus on the provisioning response of the female, the male and the helpers to the growing needs of the nestlings. We point out the individual

variations in the cooperative behaviour with regards to their status in the family. Measuring variation on the nestling care investment on a time scale defined the role of each member of the family and point out the benefits (direct/indirect) one may gain. We are interested to test if the main provider makes provisioning adjustments corresponding to the helpers' efforts on the course of a cooperative breeding of the Green Aracari. We expect the female and the male to be the main care providers at a similar level. The help provided by the three helpers should be of less intensity and should fade with time. In this system, information on the state of the brood is difficult to evaluate by the caretakers because care to the nestlings is performed inside the cavity, out of the sight of other family members. Therefore nestling feeding adjustments are ruled by the nestling needs and not by the nest attendance other providers may see.

Methods

Studied species

The Green Aracari is a small (30 cm, long) ramphastid found in the tropical lowland forest of Venezuela, Surinam and northern Brazil. Very little is about the behaviour of this species in the wild. Breeding occurs between April and June, the incubation lasts 16 days and the nestling stays in the nest 45 days, and both parents feed the nestlings (Short and Horne 2001). The presence of juvenile aracaris in the parent territory is confirmed for many species (delHoyo et al. 2002). Members of a family cell use a communal roosting site located in a tree cavity (Skutch 1958). Most ramphastids are unable to excavate a nesting cavity (delHoyo et al. 2002).

Experimental conditions

The experiment took place at the Montreal Biodôme, a museum which exhibits live representations of ecosystems found in the Americas (www.biodome.qc.ca). Among them is a 2600 m² representation of the South American rainforest. Air temperature ranges from 25 to 28°C during the day and 21 to 22°C at night. Relative humidity is at least 70%. Artificial lighting ensures a photoperiod similar to what is found under tropical latitudes (day: night = 14:10 hr. in summer gradually shifting to 13:11 hr. in winter). Various growth stages of the tropical forest are exhibited, each with the appropriate flora (trees, shrubs, palms, herbaceous plants): the mature forest, the secondary forest and the flooded forest. The fauna includes mammals, reptiles, amphibians, fishes and 50 to 60 free flying birds. The Green Aracari is a passive (non-aggressive) dominant bird at feeders. In November 2007, a breeding pair was formed by introducing a 7 year old female with the resident 13 year old male. A first reproduction successfully occurred in February 2008, producing three females who then became helpers.

During the breeding periods, four cavities were available to the aracaris. Two were wooden nest boxes, designed according to the recommended AZA specifications (Seibels and Vince 2001) located 8 meters apart. Those nesting cavity were filled with a 5 to 10 cm layer of wood chips. The third cavity was a circular PVC box (40 cm diameter X 50 cm) only used for roosting. The other cavity was an artificial exhibit element in the shape of an 18 m. deep tube with a 20 cm opening at the top. The aracaris only used the first few centimetres of this tube as roosting site for the night. After visiting all cavities (n=4), the female chose one as the nesting site. Four cavities in the experiment unit represent 15.38 cavities/ha which is 3.34 times more than the 4.6 ±3.0 /ha suitable cavities below 15 meters found in tropical primary forest of Argentina (Cockle et al. 2008).

The first breeding event occurred in 2008 where the first of a two egg clutch was laid on July 27. When the young fledged they were removed form the aviary (October

2008). All nest boxes were also removed to prevent unwanted breeding. The two remaining cavities (the PVC box and the "tube") were used on a regular basis for roosting. In 2009 the first of a three eggs clutch was laid on June 1. Data collection was ended after all nestlings fledged. On both years, incubation lasted 16 days and fledglings left the nest 40 days after hatching. We were able to monitor feeding behaviour adequately from hatchling to the first 25 days inside the nest box. Past that time, nestlings started climbing the nest wall toward the entrance of the box where they were out of the camera's field of view.

Audio visual equipment

We monitored two reproductive sequences of Green Aracari on consecutive years (2008 and 2009). To insure identification, all individuals were leg banded with different colors and equipped with an under skin passive integrated transponder (PIT), located between the scapulas (model: 134.2 kHz, ISO). Leg bands were use for direct visual identification, while PIT tags were used in conjunction with a Biomark reader (model: FS-2001) for continuous monitoring.

Following the selection of a nest box by the female, a video camera (model: WK-CIE48HVCD) was installed to record activities inside the nest box. The camera is equipped with 48 built-in infrared lights (LED) enabling recording in almost complete darkness without disturbing the birds (Pierce and Pobprasert 2007). In 2008, the camera system was coupled with the microchip reader attached to the nest box in order to confirm individual identification when leg band was not visible with the camera. In 2009, a second camera was installed outside the nest box for this purpose only, while the microchip reader was transferred to monitor the roosting cavity (the «tube») were all helpers spent the night.

The camera system was linked with security software (EZCapture 7.1, Avermedia technology Inc.) for archiving video on computer files. Video capture was automated by motion detection and was effective from 6:00 to 21:00 hr. during the entire breeding period. More than 800 hours were recorded for each breeding event in 2008 and in 2009. For this paper we viewed 375 hours of the nestling feeding period for each breeding corresponding to the first 25 days after hatching.

Breeding chronology

Over the two years of our study on aracari breeding behaviour nine clutches were laid (Table 1). The first breeding (2008.1) produced the helpers, all females. Then the second clutch laid (2008.2) was sterilised for collection managing purposes. Three more clutches were produced, but eggs were damaged. Eggs of clutch 2008.3 were removed and those of clutch 2008.4-5 were ejected by the birds themselves. It was noticed that the aging male was having a hard time getting to the bottom of the nest, and it was thought that the collision with the eggs might have damaged them, leading to their ejection. Therefore, the nest box was inclined at angle of 45° on June 23 of 2008. It is difficult to associate a particular event to the breaking of an egg. It may occur while the five individuals are roosting in the nest box or by some other cause. The ejection of the damaged eggs of clutch 2008.5 was made by a juvenile. On the sixth clutch of 2008 (2008.6) three eggs were lain, and one was damaged by another juvenile and ejected the same day. This was the second successful breeding, three helpers participated and it produced two nestlings. They were removed from the experimental unit 16 weeks after hatching. In 2009, the helpers roosted in a different cavity than the parents, the nest box was inclined and no eggs were damaged. The two first clutches of 2009 were not fertile and were removed after 18 days (2009. 1-2). The third clutch was composed of three eggs, all hatched and this time, two of the same helpers assisted their parents. In our analysis, we summed the contribution of

all juveniles under the name "helpers". The variations observed in the behaviour of each individual reflect a response induced by the different number of nestlings.

Data collection

Four stages define a breeding cycle: nest preparation, egg incubation, nestling feeding and weaning. This study focuses on the nestling feeding stage. Associated behaviour occurring outside the nest box were not monitored.

Each year, the activities of all feeding birds were followed: the female, the male and two or three female juveniles. For every bird visit at the nest box, the following data were recorded: identification of the provider, time of arrival, the number of provisions transferred to nestlings and time of departure. Based on these data, the daily visiting rate (number of visits per day), the mean duration of a visit (in seconds) and the individual nestling feeding rate (number of provisions per hour per nestling) were calculated. A provision was counted each time a provider introduced its beak into a nestling's beak to transfer food. Because the food available to aracaris was in the form of softbill pellets or diced fruits, the size of every feeding is considered normalized and equivalent. We also considered the number of provisions transferred to a nestling to be accurate and representative of the feeding effort given by an individual (Canestrari et al. 2005).

Data analysis

In our analysis, the contribution of the juveniles is summed under the name "helpers" and the effect of clutch size was controlled by adjusting our data per nestling. Since

per-nestling feeding rates were not normally distributed, non-parametric analyses were used for all comparisons.

The visiting rates, the duration of visits and the nestling feeding rates for two independent breeding events (2008 and 2009) were measured to characterize the relative efforts of the five members of a family group of Green Araçari. To compare providers for both years, we calculated the overall number of visits, the total number of feedings *per* nestling and we compared the duration of a visit with a non-parametric Wilcoxon signed rank test based on years for the female, the male and the helpers. After hatching, not all visits to the nest were made for feeding the nestlings. We therefore used Kendall's tau measure of correlation to estimate the influence of the visiting rate of the female, the male and the helpers on nestling feeding rates. The similarity of the two breeding events was assessed by comparing the overall nestling feeding rates between 2008 and 2009. This was done using a non-parametric Wilcoxon rank-sum test, performed on years for the female, the male and the helpers.

Variations of nestling feeding rates were also compared as a function of the metabolic changes observed in the nestlings. In order to compare trends between individuals, we pooled our data in three periods defined by changes in nestling morphology corresponding to nestling stages. The first period was established from the hatching of the eggs to the appearance of feathers on the nestlings' wings (day 1 to 8). The second period corresponded to the day after the appearance of feathers to the opening of the nestlings' eyes (day 9 to 20). The last period covered the day after eye opening to the day nestlings start climbing towards the nest box entrance (day 21-25). We used a Kruskal-Wallis test or a Wilcoxon rank-sum test, when appropriate, to test the statistical hypothesis of homogeneity of the feeding rates between years, periods and individuals. Significant differences between nestling stages can increase or decrease as a trend of the nestling feeding behaviour associated to an individual. Because in the cooperative Arabian Babbler (*Turdoides squamiceps*) the same provisioning rules apply to both helpers and parents (Wright 1998), we expected to

find an increasing nestling feeding rate between periods and similarity between years (N=2) and individuals (N_{2008}=5, N_{2009}=4).

Variations in nestling feeding rates were also analysed as a function of the age of the nestlings to compare feeding behaviour of cooperative individuals between years. Because food was not a limiting factor during both breeding events (2008 and 2009), we expected to have homogeneity in the nestling feeding rates between years by an individual. We analysed the nestling feeding rates with a series of Wilcoxon rank-sum test to test for significant differences associated to a specific nestling stage (day) for the female, the male and the helpers.

Comparisons between individuals were then conducted on a finer time scale by analyzing the hourly variations in provisioning. We grouped the nestling feeding rates of each bird (female, male and helpers) in blocks of one hour each from 6h to 20h. Rates of nestling feedings *per* hour were then compared using a non-parametric Wilcoxon rank-sum test to determine feeding hour peaks. The highest feeding rates were expected to be during the morning hours. It was also expected that all individuals would exhibit the same feeding profile for both years.

Results

As it occurs in the wild, the nightly attendance of three juveniles roosting with their parents in 2008 was expected even if it was the first time this behaviour was recorded in captivity. Their absence from roosting in the nest box five days after the 2008 hatching suggests the eviction by the parents, although no direct observation confirmed any altercation. Afterwards, no juvenile roosted again in the same cavity with their parents.

Overall participation

In 2008, the five members of the family made 1521 visits (female: 781, male: 247, helpers: 493) to the two nestlings and provided 2946 provisions (female: 2110, male: 145, helpers: 691; to the two nestlings). In 2009, four members of the family (one juvenile did not help) made 1792 visits (female: 1113, male: 202, helpers: 477) to the three nestlings and fed them with 4994 provisions (female: 3972, male: 126, helpers: 896). The Chi square tests of homogeneity showed that only the visit-feeding totals of the male were similar between years (Table 2.2). Only the female showed a significant variation with regard to duration of a visit; spending more time in the box per visit in 2009 ($Z= -3.1241$, $p = 0.0018$*) (Figure 2.1).

Number of visits and feeding rates

Feeding the nestlings was the only task performed by all members of the group. To determine differences between attendance at the nest and provisioning, we performed a non-parametric Kendall's correlation test on the number of visits per day and the nestling feeding rates of individuals for both years (Table 3). In 2008 and 2009, the female and helpers delivered more provisions when they made more visits, but we did not find any significant correlation between the frequency of visits and the feeding rates provided by the male. Even when the male went more often in the nest box, he did not increase his feeding of nestlings.

Yearly variations in feeding rates

We used non-parametric Wilcoxon rank-sum test to analyze the whole sequence of nestling feeding rates for both years (Figure 2.2). The total nestling feeding rates did not vary between years (Z = -0.3504; N2008= 314, N2009= 370; P=0.7260). When analysed by individuals, only the nestling feeding rates of the female showed no significant difference between years (Z=-1.0420; N_{2008}= 304, N_{2009}= 366; P=0.2974). The male and helpers had significantly lower nestling feeding rates in 2009 than in 2008 (male: Z = -8.1383; N_{2008} = 109, N_{2009} = 95; P< 0.0001* , helpers : Z = 3.2753; N_{2008} = 170, N_{2009}= 207; P = 0.0011*). The nestling feeding rate median score by the female (2008 = 3, 2009 = 3.333) was the highest, followed by the helpers (2008 = 1.5, 2009 = 1.3) and by the male (2008 = 0.5, 2009 = 0.3).

Nestling growth and associated biological periods

A growth chart base on the weight of an hand fed Green Aracaris (Figure 2.3) shows a distinctive non-linear function with age of the nestling (Holland 2008). The mass gain of the nestlings is slow for the first 5 days, but increased rapidly after 10 days. Changes in metabolic conditions of the nestlings were associated with three periods where modification of their appearance was observed. Taken separately, each period fits a linear function. The first period (A : day 1 to 8) is described by a slope of 1.22 (r^2=0.9537), the second period (B : 9 to 20) by a slope of 3.75 (r^2=0.9709) and the third period (C : day 21 to 25) by a slope of 6.46 (r^2=0.9954).

The nestling feeding rates by the female were similar between years for the three periods (Figure 2.4(a)). A significant lower nestling feeding rate by the male was found in 2009 during the three periods (Figure 2.4 (b)). Helpers did not feed any nestling during the first period of 2009, thus no statistical analyses were performed at period A. Nestling feeding rates by the helpers between years were similar at period B, but significantly lower in 2009 at period C (Figure 2.4 (c)).

The nestling feeding rates were also compared between periods for the female, the male and the helpers. In 2008, nestling feeding rates by the female and the helpers significantly increased between periods (Figure 2.4 (a), (c)). In 2009, the nestling feeding rates by the female and the helpers significantly increased between period A and B, but they were similar between period B and C (Figure 2.4 (a), (c)). The nestling feeding rates by the male were similar between all periods in both years (Figure 2.4 (b)).

The same types of comparisons were done between individuals for period A, B and C. The nestling feeding rates by the female were significantly higher than the male and the helpers in all three periods, on both breeding events (2008-2009) (Figure 2.5 (a), (b), (c)). The nestling feeding rates by the helpers were significantly higher than what we observed by the male in period B and C in both years, and it was similar in period A of 2008 (no data for 2009) (Figure 2.5 (b), (c)).

Daily variations in feeding rates between years

When comparing the nestling feeding rates by the female on a daily basis between years, all but one paired-day were similar. Her nestling feeding rates at day 14 was significantly lower in 2008 than in 2009. The nestling feeding rates by the male was significantly higher in 2008 than in 2009 on 8 occasions (day 7, 9, 12, 17, 21, 22, 23, 24). Helpers had significantly lower nestling feeding rates in 2008 than in 2009 at days 14 and 15, but higher rates in 2008 than in 2009 at day 19, 20, 21, 22 and 25 (Figure 2.6)

Hourly variations in feeding rates

All observations were grouped in one typical day separated by hour blocks from 6h to 20h. We found a significantly higher feeding rate of nestlings by the female and the helpers in the early hours and in the late afternoon periods. In the case of the female (Figure 2.7(a) and 2.8(a)), the hour blocks 7, 17 and 18 of 2008 were significantly different than the rest of the day ($Z=4.7742$; $p <0.0001$*), whereas in 2009 it was only the hour blocks 7 and 18 ($Z=5.0535$; $p <0.001$*) that were different. The helpers (Figure 2.7(c) and 2.8(c)) had higher nestling feeding rates than the rest of the day during the 7, 8 and 16 hour blocks in 2008 ($Z=2.7987$; $p =0.0051$*) and the 6, 7 and 16 hour blocks in 2009 ($Z=2.8581$; $p = 0.0043$*). When peaks of nestling feeding rates were removed, no significant variation was found during the rest of the day for the female (2008: $X^2=7.9063$; $df=10$; $p=0.6380$, 2009: $X^2= 3.0255$; $df=11$; $p=0.2917$) and for the helpers (2008: $X^2=8.2820$; $df=10$; $p=0.6013$, 2009: $X^2=6.8917$;$df=10$; $p=0.7356$). The nestling feeding rates peaks were similar within the same period for the female (2008: $X^2=4.0861$;$df=2$; $p=0.1296$, 2009: $Z=0.8118$; $p = 0.4169$) and for helpers (2008 : $X^2=0.0675$; $df=2$; $p = 0.9668$, 2009: $X^2=2.8243$; $df=2$; $p=0.2436$). The feeding rates of nestlings by the male (2.7(b) and 2.8(b)) showed no significant hourly variations for both years (2008: $X^2= 3.0465$; $df=13$; $p=0.4442$, 2009: $X^2=14.7054$; $df=13$, $p=0.2579$), and were constantly low.

Discussion

In a controlled environment without predators where food is abundant and cavity availability is not constrained, juvenile Green Aracaris assisted their parents in a cooperative breeding system. During two independent breeding events involving the same five family members, we monitored individual behaviour of all individuals (parents and helpers) to define their respective contribution in those breeding events.

While not included in our statistical analysis, visual observations confirmed that helpers fed the nestlings until they were fledged.

The female invested the most in the nestlings feeding on both years. During the nestling feeding period, the overall feeding rates were correlated with the daily visiting rates in both years. When more visits were made to the nest box, more provisions were delivered to the nestlings by the female and the helpers. However, this relationship was not significant for the male where visits to the nest were not linked to food provisioning, suggesting the variation of the nestling feeding rates cannot be assessed simply by the number of visits alone. Future studies on cavity nesters should be cautious when evaluating nestling feeding efforts by using only nest visiting rates.

The male's presence in the nest box was not related to nestling feeding but probably to vigilance or protection behaviour. The male was often seen perched in the entrance of the nest for several minutes. Because the aracari was the dominant bird in the aviary, no agonistic behaviour with other species was recorded. Thus, it is difficult to define or associate a precise role to the male, but it is clear that its implication in the feeding of nestlings was limited. Because all three helpers were females, we couldn't test the hypothesis of a sex effect of helpers on nestling feeding behaviour. Another important factor to consider was the age of the male, which was 14 year old at his first breeding in 2008. He was considered old with regards to the life table of the captive population of the Green Aracari in the management plan of this species (Willis and Bragin 2004).

Following the growth chart, the variation in the increase of the body mass between periods suggests major adjustments in the nestling provisioning, and consequently a variation in the feeding rates between periods. During the progression of the clutch, we observed an increase in the number of visits, and more provisions were delivered by the female and the helpers following the growth of the nestlings. Three periods in 2008, and two periods in 2009 were significantly different with an increasing nestling

feeding rates by the female and the helpers. We suggest that metabolic changes in the nestlings' growth may induce an increase in the energetic requirements of nestlings. Our observations are an indirect report of those morphological changes and they are somewhat synchronized with the increase of nestlings feeding behaviour. Because of the non-parametric nature of our data we could not analyze them as linear functions but the increase in nestling feeding rates between periods indicates a clear trend shared by the female and the helpers.

A pattern was also detected at the hourly level, with a peak nestling-feeding rate in the morning hours and in late afternoon hours with a low rate just before dusk. This feeding behaviour was similar in both breeding events when we controlled our data for the number of nestlings. The daily variation was expected because a temporal feeding pattern was observed for ramphastids in natural habitats (Kantak 1981). It is interesting to notice that the 7h hour block was one of the highest values of nestlings feeding rates by the female and helpers for both years. The female fed nestlings at a higher rate one or two hours before roosting while the helpers had a peak three to four hours before their last visit to the nest box. This difference in feeding hours at the end of the day might be beneficial for nestlings having a longer period of high feeding rates just before the night.

The helpers' effect was different between years. We measured a significant decrease in the overall nestling feeding rate from 2008 to 2009. This lower feeding rate was probably related with the lack of participation of one juvenile in the 2009 breeding event. This non participation could be related to the age, the social rank or mating readiness of the individual which suggests that helping behaviour fades with time in this species. The bird nevertheless shared the same roosting site with the other juveniles every night. The major difference in nestling feeding rates of the female and the helpers was the intensity of the behaviour and the timing of the help. The female maintained a nestling feeding rate at least two times higher than the rate of the helpers. The timing of the help is another important factor. Helpers did not feed the nestlings in the first days after hatching but it is clear their implication began when the

nestlings were 9 or 10 days old. Our observations outside the nest box were not sufficient to determine if helpers were restrained from entering the cavity in the first week after hatching.

The helping behaviour of juveniles is confirmed for this species but the intensity of the assistance may be without direct benefit for the breeders. Variations of the male and helpers' contributions between years, although lower in 2009, did not affect nestling feedings by the female. The variations in provisioning behaviour of the male and helpers were not sufficient to induce a proportional variation or a detectable load-lightening effect on the main provider (female). Hence, our results do not support the compensatory effect hypothesis for food provisioning resulting in no indirect benefits for the helpers. The helping behaviour seemed to fade in time. In 2009, one juvenile did not cooperate in the breeding, and a lower nestling feeding rate was observed. This could mean that helpers are replaced by the following generation from one breeding season to another.

The occurrence of cooperative breeding of the Green Aracari in captivity, when ecological constraints are released, suggest other selective pressure than cavity or food availability alone. Our study shows that helping behaviour, even if facilitated by ecological constraints in the wild, should benefit the helpers in some other aspect. Indirect benefits for helpers should be investigated by a long term study with multiple breeding. As shown by Komdeur (1996), individuals with helping experience have a greater lifetime reproductive success. It would be interesting to compare the breeding success of an individual with helping history with another without a cooperative record. A better breeding success for an experienced bird is an indirect fitness gain for the parents and a direct, but delayed, benefit for the bird itself. Long term studies are needed to provide more insight on the indirect benefits of cooperative breeding on helpers for this species. Overview of the ramphastid breeding success in Zoological institutions could provide conditions for such long term investigations that are difficult to carry in the wild.

Our research was based on observations for two breeding events of the same family group of Green Aracari in captivity. Therefore, we are aware that inferences are limited by the number of breeding events and the lack of independence in the cooperative breeding group under study. On the other hand, finding toucan nests in the wild is very difficult and very few studies have been conducted on their breeding behaviour. Studies in controlled environments might be a key to a better understanding of the biological needs of the species when experimentation in natural environments is challenging or impossible.

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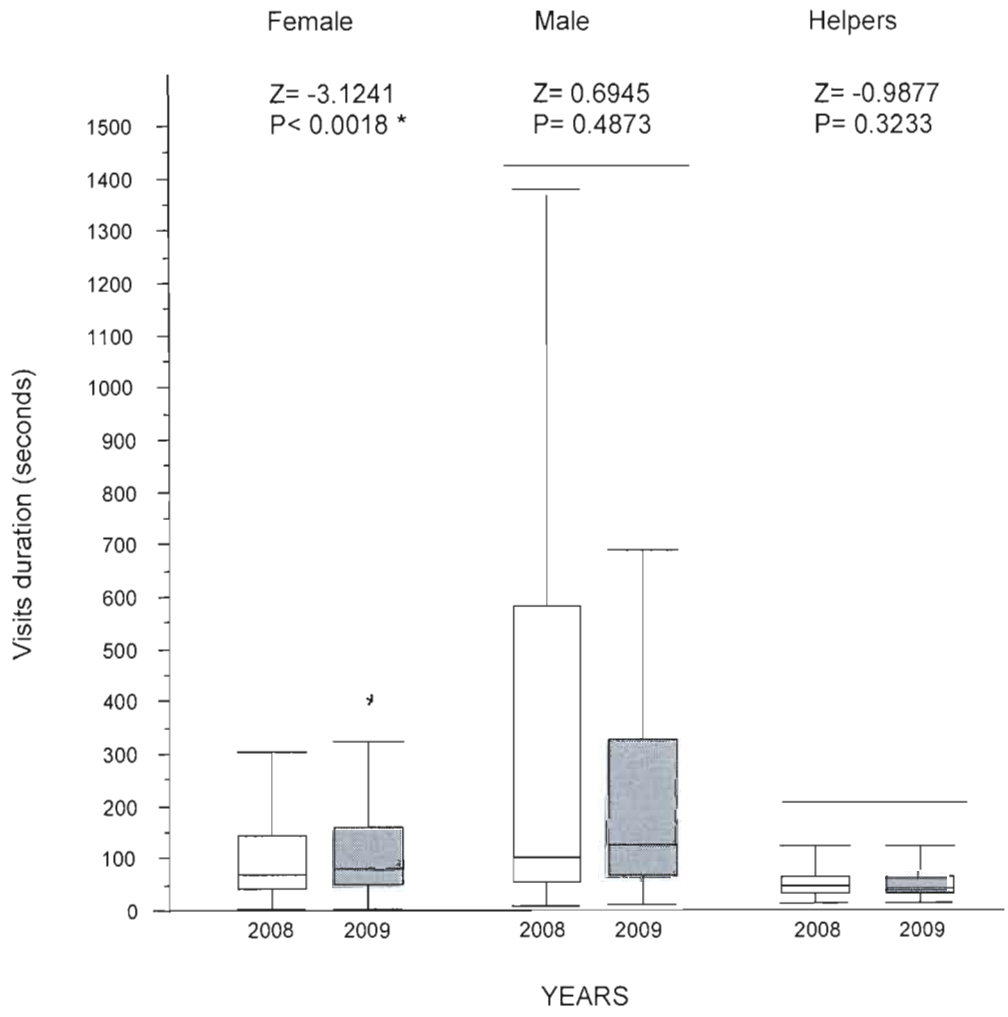

Figure 2.7 Median visits duration comparison by years for Green Aracari female (n=1), male (n=1) and helpers (n=3) from two breeding periods in captivity at the Montreal Biodôme. Box plots are quantiles of the overall variations of the duration of a visit to the nest box made by an individual for 2008 and 2009. Asterisk (*) identify the year with significantly longer visits for an individual. Solid lines represent similar visit durations.

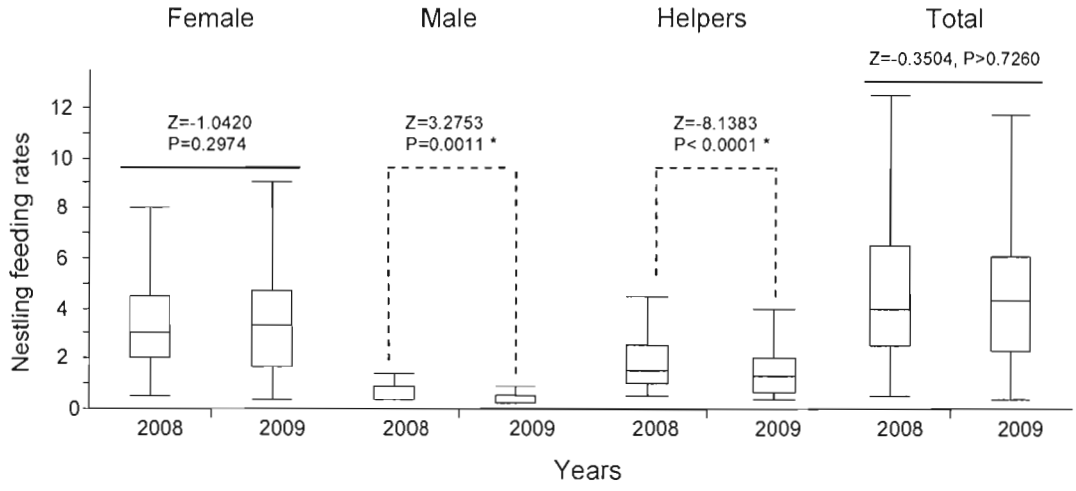

Figure 2.8 Median nestling feeding rate comparisons by years for Green Aracari female (n=1), male (n=1) and helpers (n=3) from two breeding periods in captivity at the Montreal Biodôme. Box plots are quantiles in number of provisions delivered per nestling per hour. Asterisk (*) identify nestling feeding rates significantly different between years. Solid lines represent similar nestling feeding rate.

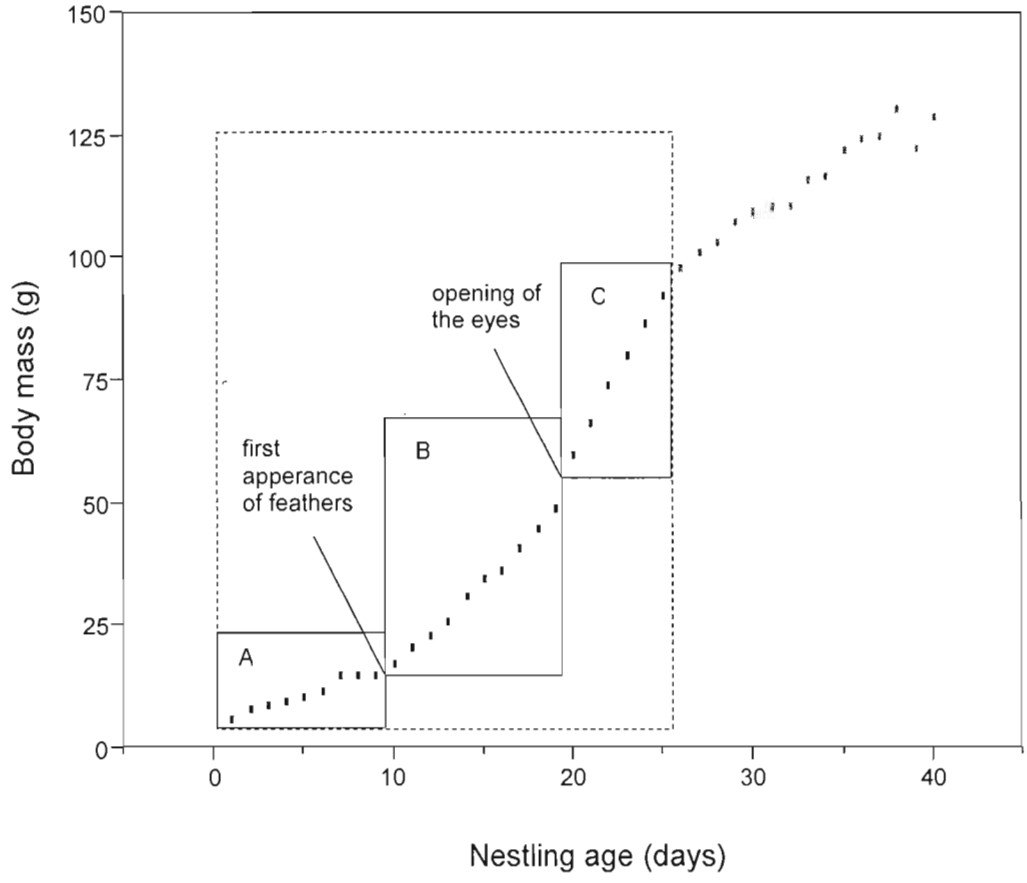

Figure 2.9 Growth chart of the Green Aracari nestling after data from the Toucan husbandry manual for the piciformes AZA TAG (Seibels and Vince 2001) . Dots indicate body mass weight as a function of the age of a nestling. Dotted square shows the range of present study and first observation of two morphological changes are indicated by solid lines. Squares A, B and C indicate nestlings' growth periods.

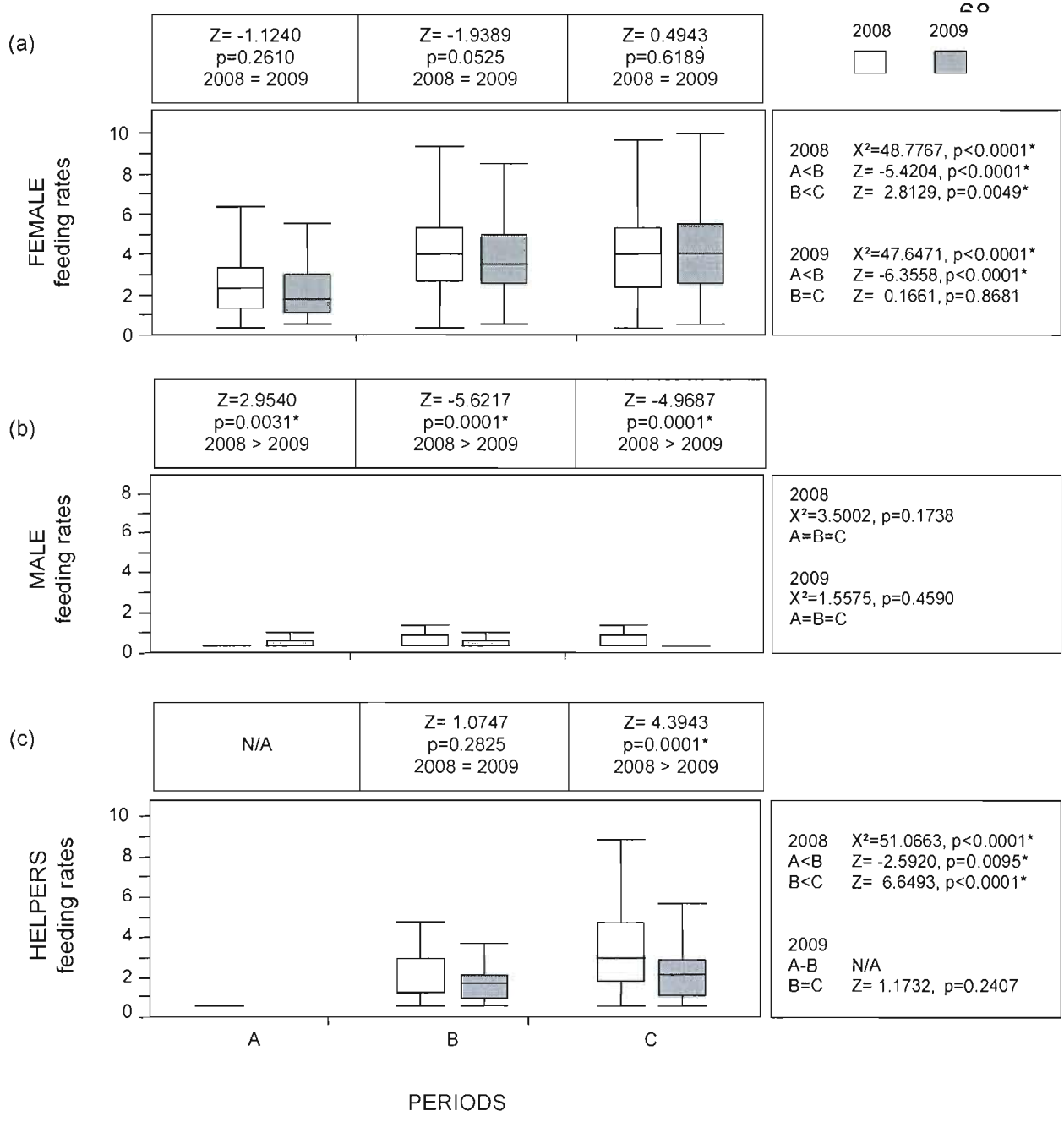

Figure 2.10 Variation in nestling feeding rates made by the female, the male and the helpers by growth periods and years. Box plots are quantiles of the feeding rates calculated in number of provisions delivered per nestling per day, pooled by periods for 2008 and 2009.

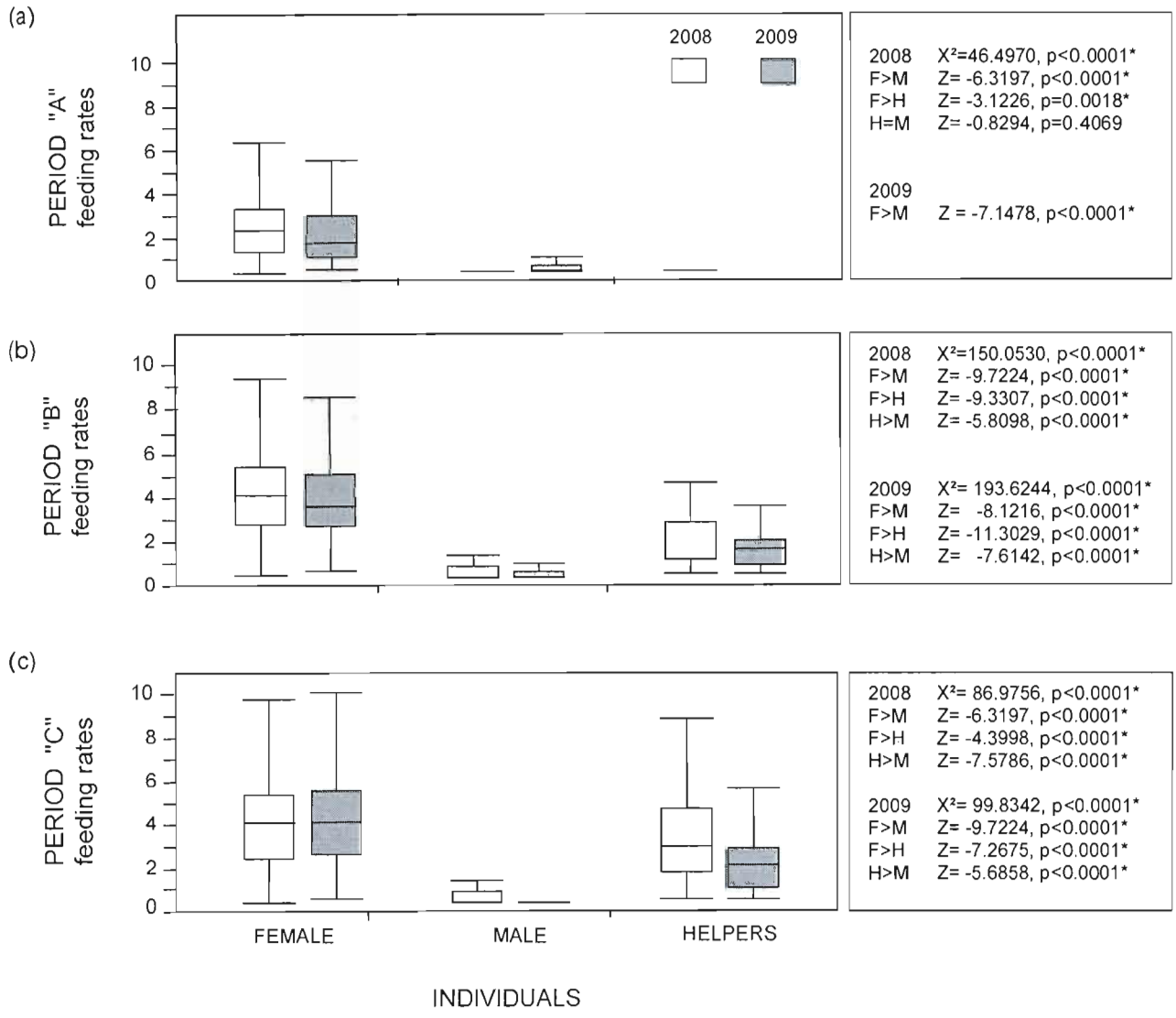

Figure 2.11 Variation in nestling feeding rates on period A,B and C by individuals and years. Box plots are quantiles of the feeding rates calculated in number of provisions delivered per nestling per day, pooled by periods for 2008 and 2009.

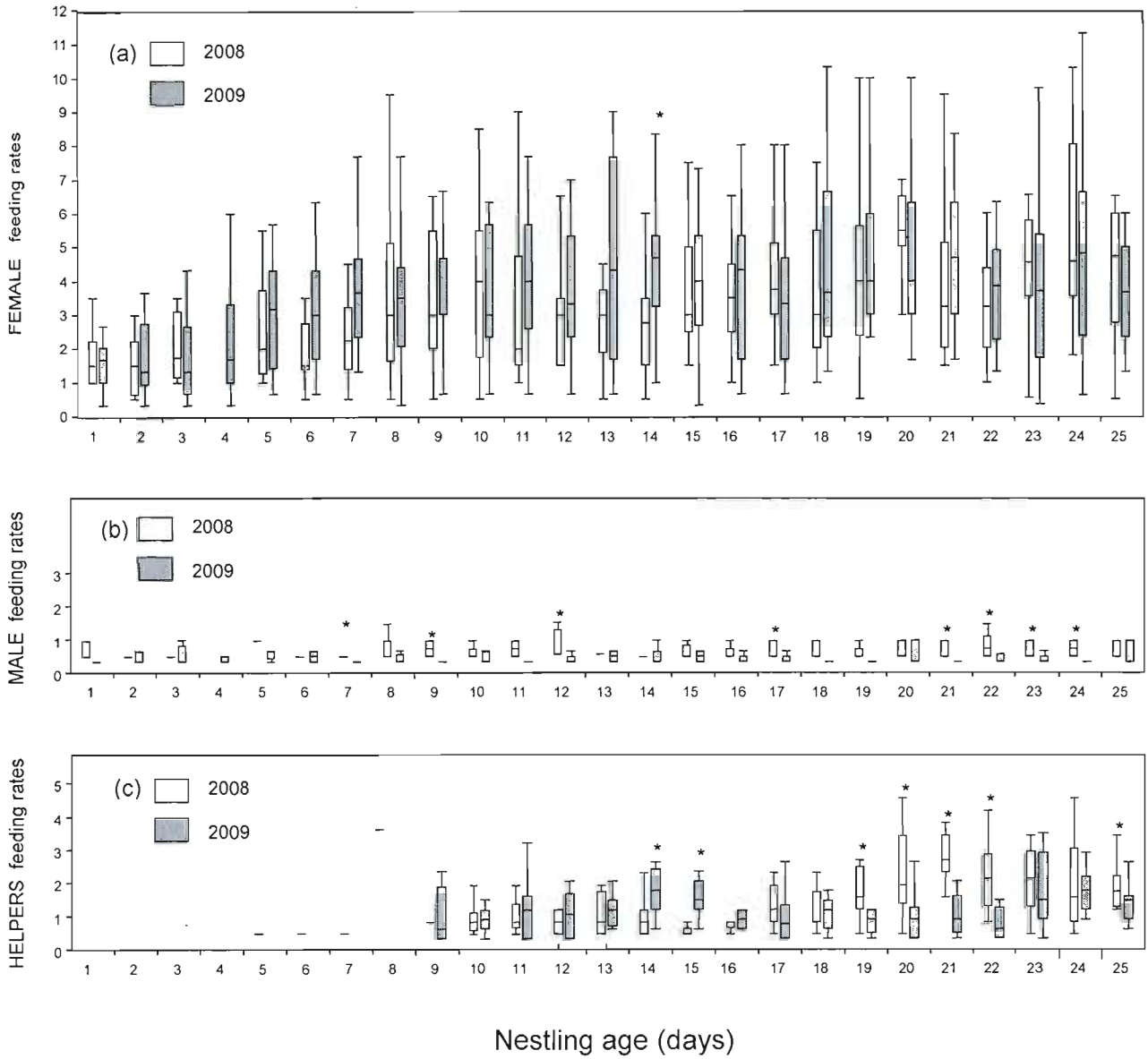

Figure 2.12 Daily variations in nestling feeding rates made by the female, the male and the helpers, between years and by the age of the nestlings. Box plots are quantiles of the feeding rates calculated in number of provisions delivered per nestling per day for 2008 and 2009. Asterisks (*) identify significant differences between years for a given day.

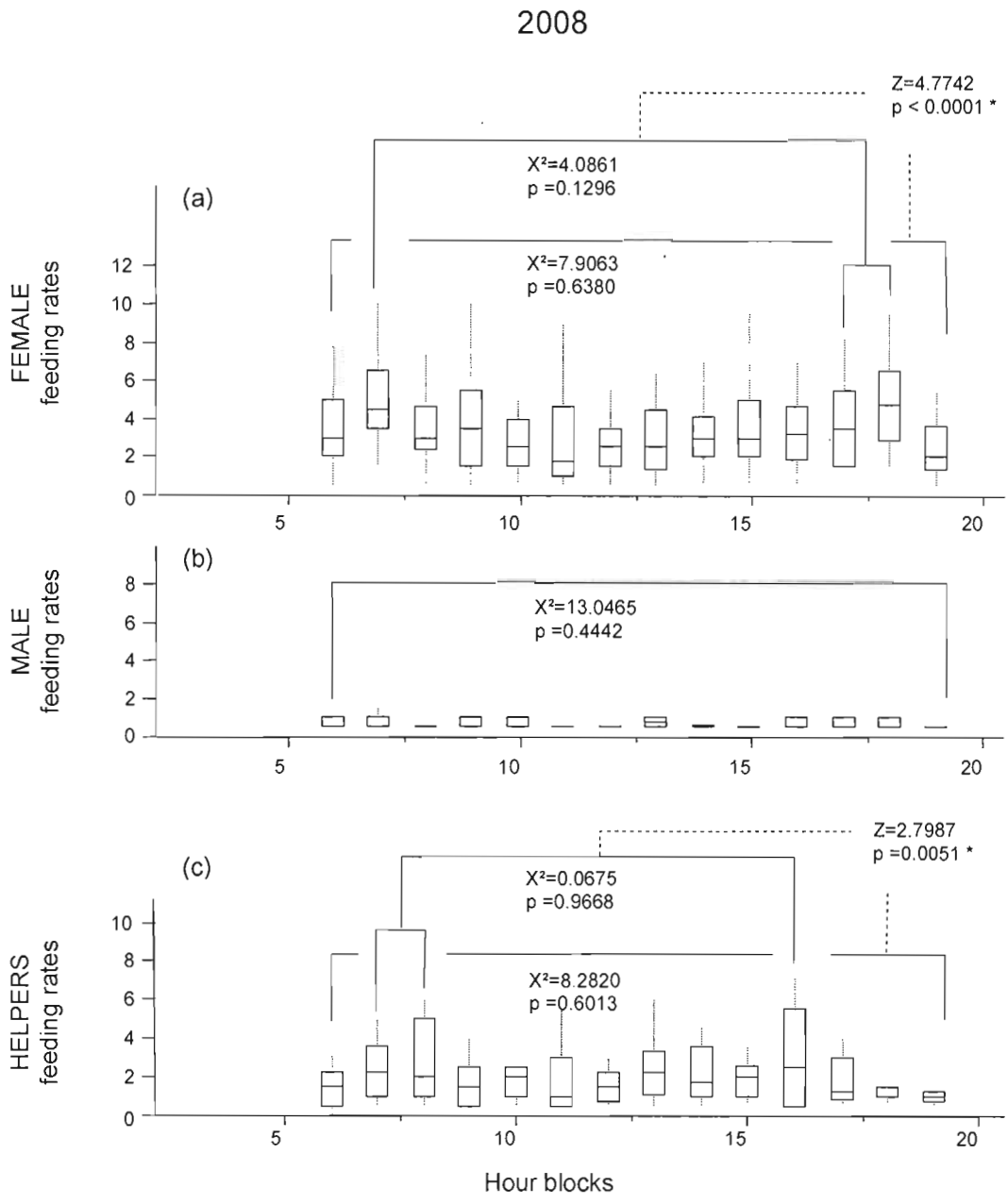

Figure 2.13 Hourly variation in nestling feeding rates 2008. Box plots are quantiles in number of provisions delivered per nestling per hour. Solid lines represent similar nestling feeding rates. Significant differences are shown by dotted lines. Asterisks (*) identify hour block significantly different than of rest of the day.

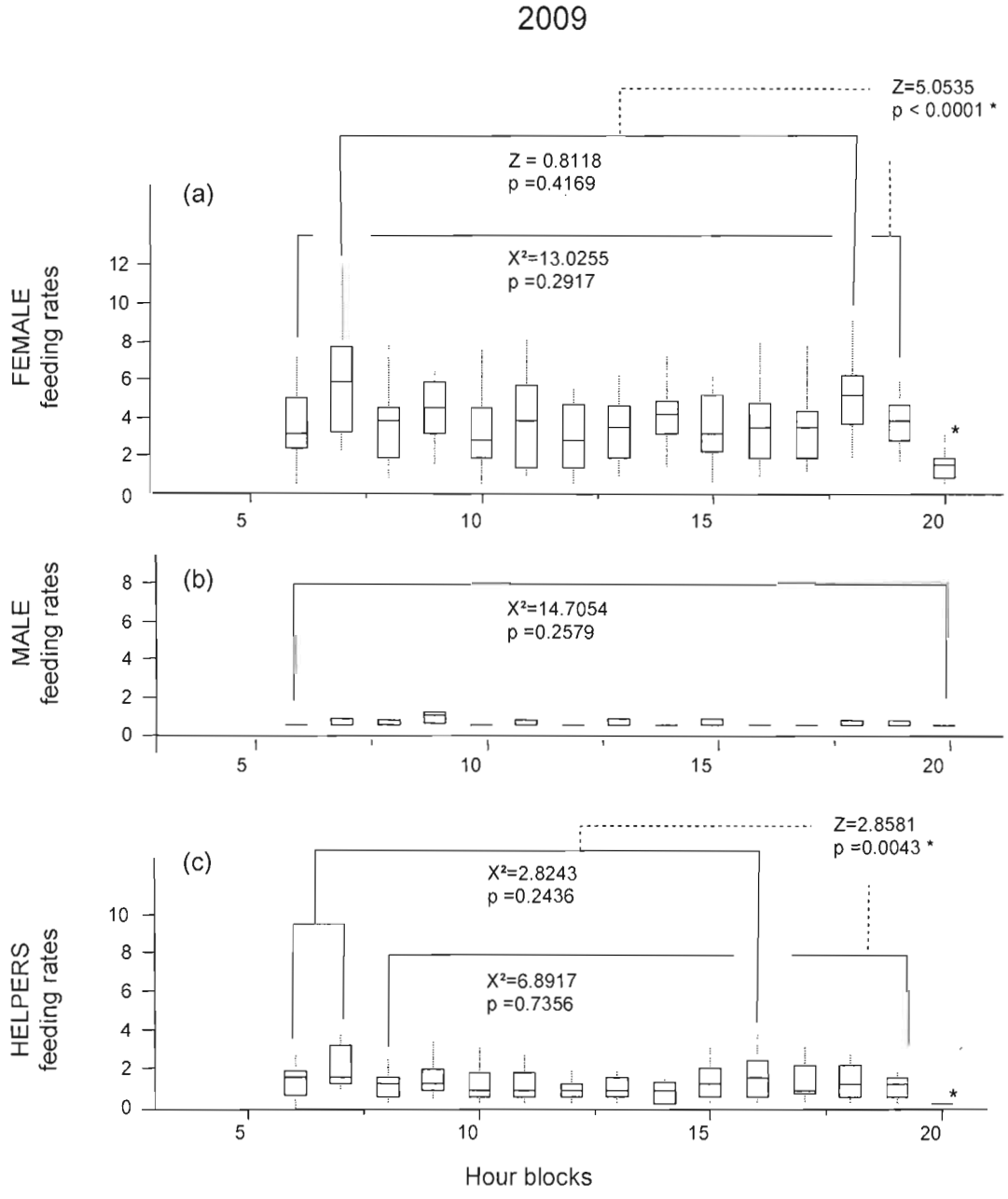

Figure 2.14 Hourly variation in nestling feeding rates 2009. Box plots are quantiles in number of provisions delivered per nestling per hour. Solid lines represent similar nestling feeding rates. Significant differences are shown by dotted lines. Asterisks (*) identify hour block significantly different than of rest of the day.

Clutch #	First egg laid	Hatch	Fledging	End of clutch	Notes
2008.1	25-12-2007	11-01-2008	22-02-2008		Helpers (3 females)
2008.2	30-03-2008	•	•	05-03-2008	eggs removed
2008.3	21-04-2008	•	•	27-04-2008	eggs ejected
2008.4	02-06-2008	•	•	14-06-2008	eggs ejected
2008.5	01-07-2008	•	•	17-07-2008	eggs ejected
2008.6	27-07-2008	12-08-2008	21-09-2008		2 chicks
2009.1	15-04-2009	•	•	05-05-2009	eggs removed
2009.2	15-05-2009	•	•	22-05-2009	eggs removed
2009.3	01-06-2009	17-06-2009	27-07-2009	25-08-2009	3 chicks

Table 2.4 Clutch chronology of a captive Green Araçari breeding pair (n=1) at the Montréal Biodôme in 2008-2009. Helpers (n=3) were kept in the aviary with breeding pair at all time from hatching to December 2009

Behaviour	Years	F	M	H	TOTAL	X^2	Prob.
# visits	2008	781	247	493	1521	281.799	<0.0001*
	2009	1113	202	477	1792	731.05	<0.0001*
# provisions	2008	2110	145	691	2946	2095.35	<0.0001*
	2009	3972	126	896	4994	4975.249	<0.0001*
X^2		26.756	0.154	12.845			
Prob.		<0.0001*	0.6947	<0.0001*			

Table 2.5 Homogeneity test of the total number of visits and number of provisions by individuals for Green Aracari female (n=1), male (n=1) and helpers (n=3) from two breeding periods in captivity at the Montreal Biodôme. Chi square values and probability tested for homogeneity by individuals (df = 2) and years (df=1). F=female, M=male, H=helpers.

Year	Individual	Tau	Prob.
2008	Female	0.4967	0.0015 *
	Male	0.0146	0.9304
	Helpers (3)	0.8433	< 0.0001*
2009	Female	0.5525	0.0002*
	Male	0.0859	0.5796
	Helpers (2)	0.6868	0.0002*

Table 2.6 Kendall tau correlation between the number and the duration of visits for Green Aracari female (n=1), male (n=1) and helpers (n=3) from two breeding periods in captivity at the Montreal Biodôme. Data range from hatching to day 25 of each breeding events.

CONCLUSION

Pour qu'une étude en captivité puisse être indicatrice d'un comportement naturel, elle doit cibler une caractérisitque qui maintient ou favorise l'expression de ce comportement. Dans notre étude, la disponibilité des cavités était l'élément pivot qui permettait de tester l'effet de la principale contrainte écologique sur les comportements d'assistance associés à la reproduction d'un utilisateur secondaire de cavité (qui ne creuse pas sa cavité), au moyen d'un environement contrôlé recréé dans un milieu artificiel. Nous nous attendions à ce que la disponibilité des cavités affaiblisse l'unité familiale de cinq Araçari vert et qu'il en résulte une absence de coopération des juvéniles à la reproduction de leurs parents.

La participation des assistants à la reproduction de leurs parents en captivité s'est déroulée sur deux années consécutives et en présence de quatre cavités sur un territoire de 2600 m². La reproduction coopérative n'avait jamais été décrite pour cette espèce et elle a rarement été observée en nature chez les ramphastidés (Skutch 1958, Berg 2001).

Les contraintes écologiques

Même si les aracaris sont incapables de creuser entièrement leur cavité, un travail d'aménagement est nécessaire (delHoyo et al. 2002). Les cavités ne sont pas distribuées équitablement dans le milieu et leur disponibilité est également liée à l'abondance des autres espèces cavicoles (Cornelius et al. 2008). On rapporte plusieurs nids d'araçaris dans le bois mort (Skutch 1958, Berg 2001, Cockle et al. 2008) ce qui suggère une durée d'utilisation limitée. Même dans un milieu où les ressources alimentaires sont abondantes, il est possible qu'un cavicole secondaire, comme l'Aracari vert, souffre de la disponibilité d'un gîte et d'un site de reproduction.

Cette disponibilité de cavités influence alors la dispersion des juvéniles qui seront portés à rester sur le territoire parental lorsque la disponibilité est faible (Ekman et al. 2004). En nature, l'observation de plusieurs individus à un gîte est commune chez les aracaris (Skutch 1958, Short and Horne 2001). Bien qu'aucune étude n'a confirmé des liens parentaux entre les individus utilisant la même cavité, nous sommes portés à croire qu'il s'agirait de parents accompagnés de leurs descendants comme c'est le cas chez d'autres oiseaux cavicoles (Lennartz et al. 1987, Ligon et al. 1988). Dans notre étude, nous avons accepté *a priori* que la disponibilité des cavités agit sur l'expression des comportements coopératifs, puisqu'elle est à l'origine du maintien des juvéniles sur le territoire parental.

En captivité, nous avons observé que même avec une forte disponibilité de cavités, les juvéniles partagent le gîte des parents au moins jusqu'à l'éclosion de la nichée suivante. Suivant cet événement, les juvéniles ont quitté le site de nidification et ont partagé le gîte dans une autre cavité.

Le profil de l'assistance

Nous avons constaté que la participation aux soins des oisillons par la femelle était élevée dans toutes les étapes de la reproduction. L'implication des assistants, ainsi que la participation du mâle, ont probablement peu d'impacts sur la survie des oisillons. Nous savons que la présence d'assistants (juvéniles) n'est pas essentielle à la reproduction de cette espèce. Par ailleurs, nos analyses confirment que la variation de l'approvisionnement des oisillons par les assistants et le mâle n'est pas compensée par la femelle qui maintient un ratio d'approvisionnement stable d'une nichée à l'autre.

La participation du mâle se manifeste par sa présence au nichoir. Il participe à l'incubation des œufs et maintient une durée de visites élevées lorsque les oisillons n'ont que quelques jours. La position qu'il adopte en couvant les oisillons, favoriserait probablement leur isothermie durant cette période. Bien que nous n'ayons pas observé de comportements de défense territoriale, la présence du mâle au nid aurait probablement un effet dans la protection de la cavité contre les prédateurs.

Pour ce qui est des assistants, leur participation négligeable lors des dix premiers jours suivant l'éclosion soulève des questions. Est-ce que la présence du mâle à l'intérieur du nichoir aurait limité les comportements de nourrissage des assistants ? Est-ce qu'un parent contrôlait l'accès au nichoir par une surveillance extérieure ? Est-ce que les assistants étaient stimulés par la présence d'oisillons au nichoir même s'ils ne pouvaient les voir de l'extérieur ?

La participation des juvéniles (assistants) à l'approvisionnent des oisillons suivait, à moindre intensité, une croissance similaire à celle de la femelle. Par ailleurs, nous savons que l'approvisionnement des oisillons est régi par le quémandage des oisillons eux-mêmes (Wright 1998) et que les signaux de quête d'un oisillon sont représentatifs de son état de satiété (Cotton et al. 1996). Puisque les individus qui nourrissent les oisillons sont soumis aux mêmes règles d'approvisionnement, nous retrouvons un profil d'assistance comparable à celui de l'approvisionneuse principale, la femelle.

Nous devons souligner que tous les assistants de notre étude étaient toutes des femelles. Les différences entre l'approvisionnement du mâle et de la femelle nous portent à croire que l'assistance au nourrissage des juvéniles aurait pu être différente si les juvéniles avaient été des mâles. D'autres travaux avec des assistants de sexe mâle et femelle permettraient de tester cette hypothèse d'une différence en fonction du sexe de l'assistant.

Nous avons constaté que la fréquence de nourrissage augmente en fonction de l'âge des oisillons et probablement en fonction de leur besoins métaboliques. Un profil d'approvisionnement journalier a été décrit. Il se présente sous la forme de deux pics de nourrissage soit un le matin et un autre en fin d'après midi. Dans l'analyse de ce profil d'approvisionnement, il faut garder en mémoire que dans notre unité expérimentale, la nourriture était toujours disponible et abondante. En milieu naturel, la répartition inégale des arbres fruitiers, la disponibilité des fruits mûrs et la compétition pour ces ressources influencent l'alimentation des frugivores (Kantak 1981) et pourraient jouer un rôle important dans l'approvisionnement des oisillons. À ce niveau, il serait intéressant de vérifier si un effet compensatoire de l'assistance serait présent lorsque l'approvisionnement des oisillons devient instable.

La non-participation d'un juvénile à la seconde reproduction suggère que les comportements d'assistance s'atténuent avec le temps. Un phénomène de remplacement des assistants d'une génération à l'autre est une hypothèse à vérifier. L'échantillonnage sur plusieurs années est nécessaire afin de montrer la dynamique de la participation des assistants. L'étude devrait se faire en milieu naturel où des territoires libres permettent la dispersion des assistants de première génération.

L'histoire naturelle de l'espèce

En réduisant la portée des contraintes écologiques, nous cherchions à faire ressortir l'expression des comportements liés à l'histoire naturelle de l'Araçari vert. Puisque nous avons montré la présence de comportement coopératif en abondance de cavités, nos analyses appuient l'hypothèse que la reproduction coopérative peux être dissociée des contraintes écologiques qui influencent la dispersion des juvéniles (Pruett-Jones 2004). L'histoire naturelle de cette espèce serait donc en partie à l'origine de ces comportements. L'Araçari vert partage des caractéristiques avec d'autres espèces coopératives qui le prédispose à des comportements altruistes

comme une longévité élevée, un développement lent des oisillons (45 jours) et une résidence annuelle sur un territoire donné (Pruett-Jones 2004). Il est difficile de prévoir quelles espèces pourraient s'adonner à des comportements coopératifs, mais en intégrant les interactions écologiques et l'histoire naturelle des espèces, nous pourrons mieux comprendre les pressions sélectives qui maintiennent la reproduction coopérative chez certaines espèces (Hatchwell and Komdeur 2000). Puisque la reproduction coopérative a également été observée chez le Cabézon toucan (*Semnornis ramphastinus*) (Restrepo and Mondragòn 1998), nous soulevons la possibilité que ce comportement puisse avoir une origine ancestrale présente dans la lignée évolutive des ramphastidés (Ligon and Burt 2004) et qu'il serait maintenu, du moins en partie, par les contraintes écologiques et par les bénéfices que peuvent en retirer les individus.

Les bénéfices

Compte tenu de nos analyses, basées sur un seul couple, il nous a été impossible de mesurer des bénéfices qui seraient associés à une reproduction coopérative. Étant donné que la femelle n'a pas compensé pour les variations du ratio d'approvisionnement entre les reproductions (2008 - 2009), elle ne semble pas avoir profité d'un bénéfice direct associé à un allègement du fardeau que représente l'approvisionnement des oisillons.

Il ne semble pas non plus que nous soyons en présence de parents népotistes qui contrôleraient l'accès à la nourriture ou à des lieux précis. Aucun comportement antagoniste n'a été rapporté dans l'unité expérimentale entre les individus au cours des périodes d'échantillonnages (plus de 1500 heures d'enregistrements vidéo en continu pour les deux événements de reproduction). Les juvéniles s'alimentaient librement et occupaient toute la surface disponible.

La comparaison avec une reproduction sans assistants aurait donné un autre point de comparaison qui aurait pu mettre en perspective un certain bénéfice pour les parents. Cette situation n'a pas été possible dans le cadre de cette étude. De plus, il aurait été intéressant de mesurer le succès reproducteur des assistants après leur participation à la reproduction de leurs parents. Le développement de l'habilité à nourrir peut être un gain en valeur adaptative s'il conduit à un meilleur succès de reproduction des assistants dans le futur. Enfin, même si la participation des assistants ne procure pas un meilleur succès de reproduction au couple focal, ni aux assistants eux-mêmes, il se peut qu'en nature, leur taux de survie soit amélioré simplement par leur présence sur le territoire parental ; un bénéfice philopatrique (Stacey and Ligon 1991, Kokko and Lundberg 2001, Russell 2001).

Même si on ne peut identifier clairement les bénéfices en termes de valeur adaptative qui pourraient maintenir l'expression de la reproduction coopérative chez l'Araçari vert, nous ne pouvons mettre de côté l'importance des liens familiaux chez cette espèce et probablement chez plusieurs ramphastidés. En captivité, cette information est majeure puisqu'elle pourrait influencer les recommandations du groupe consultatif de ce taxon (Piciformes Taxon Advisory Group) concernant les lignes directrices de garde en captivité ; à savoir le maintien de groupes familiaux plutôt que d'individu seul. En milieu naturel, les araçaris sont l'objet de préoccupations mineures selon la liste rouge de l'IUCN. Toutefois, si une intervention humaine devenait nécessaire, nos travaux indiquent que l'utilisation de nichoirs dans les efforts de conservation ne nuirait pas à l'expression des comportements coopératifs chez l'Araçari vert. Des nichoirs augmenteraient la disponibilité des cavités et favoriseraient l'établissement de populations stables dans des secteurs ciblés.

AUTORISATION POUR L'UTILISATION DES ANIMAUX EN RECHERCHE

UNIVERSITÉ DU QUÉBEC À MONTRÉAL
COMITÉ INSTITUTIONNEL DE PROTECTION DES ANIMAUX (CIPA)

FICHE DE PROTOCOLE

Chercheur principal :	Pierre Drapeau
Département / Compagnie:	Sciences biologiques
Titre du projet :	*Étude du rôle des juvéniles dans la reproduction de l'Araçari vert au Biodôme de Montréal*
Référence de protocole :	0609-654-0610

Ce protocole est valide jusqu'au 30 juin 2010. Sa catégorie invasive de recherche est B (Expériences causant peu d'inconfort ou de stress).

Conformément aux directives du Conseil canadien de protection des animaux (CCPA), votre protocole sera revu et approuvé annuellement par le CIPA, et ce jusqu'à trois reprises. Par suite, le présent protocole pourra être renouvelé trois fois. Toute demande de modification *mineure* à ce protocole devra être acheminée à l'attention de madame Catherine Jumarie, ainsi qu'à celle de madame Manon St-Germain. Une modification *majeure* nécessitera le dépôt d'une demande à cet effet auprès du CIPA. **Prenez note qu'une variation de plus de 15% (jusqu'à un total de 40) du nombre indiqué ci-dessous constituera une modification majeure à votre protocole.**

NOMBRE D'ANIMAUX AUTORISÉS

Espèce	Souche	Sexe	Âge ou poids	Nombre
Araçari vert		M	13 ans	1
Araçari vert		F	8 ans	1
Araçari vert		F	16 mois	3
Araçari vert			oisillons	3 max (1 couvée)

Catherine Jumarie Présidente du CIPA	Pascale Martineau Coordonnatrice CIPA
C. Jumarie	

Date : le 2 juin 2009

AUTORISATION DE REPRODUIRE L'ARAÇARI VERT AU BIODÔME DE MONTRÉAL

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P.S.Animalier, Collections vivantes
Biodôme de Montréal

Serge Pepin
Curator of Animal Collections
Biodôme de Montréal

The pairing of studbook numbers 157 and 286 is still a high priority for the North American Regional population of the green aracari. Furthermore, your research could prove extremely informative and beneficial for the management of the population. If offspring can be successfully kept with their parents while subsequent clutches of offspring are raised, this could effectively increase the amount of spaces available for this species in North American collections. A larger population would allow a slower rate of loss of genetic variation from the population. Even if it turns out that it is not possible for adults to successfully raise offspring in the presence of older siblings, this research would then demonstrate the importance of removing offspring from their parents' enclosure when attempting to produce subsequent clutches.

I hope your research project goes well.

Kevin Willis
Green Aracari Studbook Keeper/Population Manager
and/ Director of Biological programs
Minnesota Zoo
13000 Zoo Blvd
Apple Valley, MN 55124

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